Assessing the interaction between history of usage and plant invasions:

Bamboo as a case study

Dissertation presented for the degree of Doctor of Philosophy in the Faculty of Science at Stellenbosch University

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Declaration

By submitting this dissertation electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights, and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

This dissertation includes three articles published with me as lead author, and one article submitted and under review, one paper published as a conference proceeding, and one paper yet to be submitted for publication. The development and writing of the papers (published and unpublished) were the principal responsibility of myself. At the start of each chapter, a declaration is included indicating the nature and extent of any contributions by co-authors. During my PhD studies I have also co-authored three other journal papers, have one article in review, and published one popular science article; these are not included in the dissertation .

Susan Canavan

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December 2018

Abstract

Studies in invasion science often focus on the biological or environmental implications of invasive alien species. However, biological invasions are inherently due to the human-mediated dispersal of species; this means that there needs to be a greater focus on the socio-economic context of why species have been introduced by humans, and how humans have created environments or situations to foster the success of alien taxa. This dissertation explores the interaction of human usage and plant invasions using bamboos as a case study, with the intention of answering the following questions: Why are some species selected by humans over others? How does this influence invasion success, impacts, and the cultural role of alien species in receiving environments?

I found that, like many other alien taxa, the transfer of bamboos globally has been non-random. Large-statured Asiatic species and those with a greater number of cultivars are more likely to have been introduced outside of their native ranges. The species with high introduction rates are the bamboos that are found to be invasive; this supports the notion that propagule pressure is a universally important factor in facilitating invasions. However, in contrast to many other studies, biogeographic status (the native status) of bamboo was not a strong predictor of the type and magnitude of impacts. Impacts are rather explained by certain human activities (disturbance such as logging and clearing, increasing temperatures related to climate change, and the promotion of bamboo monocultures in mixed forests for commercial purposes). As such, the management of highly competitive native species should be considered in conjunction with the management of invasive alien species in forest ecosystems where bamboos are present.

The competitive nature of bamboos that leads to impacts can be applied to other tall-statured grasses. Specifically, rapid growth rate and the capacity to accumulate biomass (a function of height) allow many tall grasses to form monospecific stands, accumulate dense and deep litter mats, reduce light availability and alter fire and nutrient-cycling regime. Naturalisation rates are greater in tall-statured grasses compared to other grasses, and the pathways of introduction are generalizable (e.g. for addressing environmental problems). Tall-statured grasses are a useful functional group for predicting high-risk taxa and for making generalised management plans.

Looking at South Africa as a case-study, I found 26 alien species of bamboo recorded as introduced, with populations of several species widely naturalised around the country. I also found bamboos to be an inherently difficult group to identify to the species level, emphasizing the caution that must be taken with regard to future introductions. Amongst the public there is a complex tapestry of perceptions towards bamboos related to (1) a long history of introduction, and multiple introduction events, where bamboos have become culturally significant for some groups of people, and (2) the realisation that they can cause problems.

In conclusion, many bamboos can be classified as synanthropic species in that they have benefited from human activity or the habitats that humans create around them. Studying bamboos has provided further insights into how social and economic imperatives are shaping a new biota at a global level.

Opsomming

Die implikasies op die omgewing en ander biologiese sisteme is gewoonlik die fokus van meeste indringer studies. Tog is hierdie biologiese indringing die gevolg van menslik-bemiddelde verspreiding van spesies. Daar moet dus meer fokus wees op die sosio-ekonomiese konteks van waarom spesies deur mense ingebring word, en ook op hoe mense situasies en omgewings geskep het om hierdie uitheemse taksa te bevorder. Bamboes word as gevallestudie gebruik om die interaksie van menslike gebruik en plantindringing te ondersoek. Die tesis poog om die volgende vrae te beantwoord: Waarom word sommige spesies bo ander gekies? Hoe beïnvloed dit die sukses van die indringing, die impak, en die kulturele rol van uitheemse spesies in die betrokke omgewings?

Ek het gevind dat die inbring van bamboes wêreldwyd nie eweredig oor spesies versprei was nie, soos met baie ander uitheemse taksa. Groot Asiatiese spesies en dié met meer kultivars word meer gereeld buite hul natuurlikke streke aangeplant. Die bamboes spesies met ‘n hoë aanvraag vir invoer is die wat indringers geword het. Dit ondersteun die idee dat propagule druk 'n universeel belangrike faktor is vir indringers. In teenstelling met baie ander studies was bamboes se biogeografiese status (die natuurlikke streek van voorkoms se klimaat en omstandighede) nie 'n goeie voorspeller van die tipe en grootte van impak nie. Impakte word eerder verklaar deur sekere menslike aktiwiteite (versteuring soos afkap, klimaatsverandering se stygende temperature, en kommersiële bamboesmonokultures in gemengde woude). Daarom moet hoogs mededingende inheemse bamboes spesies se bestuur ook oorweeg word net soos vir indringer spesies.

Hierdie mededingende aard van bamboes wat impakte veroorsaak, kan toegepas word op ander groot en lang (hoë) grasse. Spesifiek, die vinnige groeitempo en die kapasiteit om biomassa op te bou ('n funksie van hoogte) laat baie lang grasse toe om monospesifieke stande te vorm, digte en diep komposmatte op te bou, ligindringing te verminder en vuur- en voedingstof-siklusse te verander. Lang grasse se naturalisasie tempo is hoër in vergelyking met ander grasse, en die meganismes van inbringing is ook veralgemeenbaar wanneer daar bv. gekyk word na die aanspreek van omgewingsimpakte. Ek argumenteer dat lang grasse 'n nuttige funksionele groep is vir die algemene bestuur en risiko voorspelling van hoërisiko-grasse.

Deur na Suid-Afrika te kyk as ‘n gevallestudie, het ek 26 uitheemse bamboespesies gekry, met populasies van verskeie spesies wat genaturaliseer het. Ek het ook gevind dat bamboes 'n inherente moeilike groep is om tot spesievlak te identifiseer, wat die waaksaamheid met verderre invoere beklemtoon. Die publiek het ‘n komplekse tapisserie van persepsies teenoor bamboes wat verband hou met (1) die besef dat hulle probleme kan veroorsaak, en (2) waar bamboes kultureel betekenisvol geword het vir sommige groepe mense vanwee 'n geskiedenis en gebruike.

Ter afsluiting kan baie bamboes as sinantropiese spesies geklassifiseer word omdat hulle voordeel trek uit menslike bemiddeling, aktiwiteit en gewoontes rondom bamboes. Die studie oor bamboes het verdere insig gegee in hoe sosiale en ekonomiese behoeftes 'n nuwe biota op globale vlak vorm.

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[CHAPTER 2]
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[CHAPTER 3]
Canavan, S. Kumschick, S. Le Roux, J.J., Richardson, D.M.˙ Wilson, J.R.U. Does origin determine environmental impacts? Not for bamboos. (2018) *Plants, People, Planet*. doi:10.1002/ppp3.5

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[CHAPTER 5]
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1 Introduction

1.1 BIOLOGICAL INVASIONS

The increase in the mobility of humans, global trade and degradation of natural areas has been a major factor in the breaching of natural boundaries of species leading to biological invasions (Meyerson and Mooney 2007). The world's biota is being reshuffled at an accelerating rate and biological invasions are becoming a major component of global change (Bardsley and Edwards-Jones 2006, Simberloff 2013). A recent global review of the movement of taxa suggests that the introduction of alien species is higher than ever (Seebens *et al.* (2017).

Biological invasions have created a global-scale natural experiment in biogeography, and as such, study of invasions or invasion science, is a rapidly growing field of research (Richardson 2006). Studying facets of invasions offers an excellent opportunity to explore ecological and evolutionary processes. The major focus of research has been on the biological factors that influence invasiveness (such as species-based mechanisms like fast-growth rates, phenotypic plasticity, ecological competence etc.), environmental factors in receiving ecosystems, as well as quantifying the impacts of human-mediated dispersal events (Catford *et al.* 2009). A number of hypotheses exist as to why invasive alien species can have such pronounced competitive advantages over native species. Specifically, their ability to reproduce in greater volumes than would be possible in their native range where they evolved might be explained by novel weapons (i.e. alien species have biochemicals that native species have never encountered (Callaway and Aschehoug 2000, Callaway and Ridenour 2004)), the enemy release hypothesis (i.e. alien species are liberated from their specialist consumers (Elton 1958, Keane and Crawley 2002); and the empty niche hypothesis (i.e. the recipient ecosystem is unsaturated, and introduced species can take advantage of unused resources; (Elton 1958, MacArthur 1970)). All of these are nested in ecological theory.

Less attention has, however, been given to the factors that influence the intentional introduction of species, and how human activity fosters invasions, e.g. the socio-economic contexts that drive biological invasions (Perrings *et al.* 2000, Perrings *et al.* 2002). Given that the introduction of many invasive alien species is not by accident, but deliberate, the decisions and economic imperatives driving the movement of alien species is shaping a new geographic composition of biota. Therefore, studying taxa that are both of value to humans and are invasive species offer an

excellent opportunity to address basic research questions on the non-random assortment of invasive alien species. Such information is crucial for making predictions on where new introductions may come from, which species might be introduced, and the underlying reasons to predict and prevent new introductions of high-risk taxa that may be future invaders.

1.1.1 The invasion process for cultivated plants

For a species to be introduced and become invasive, a number of barriers must be overcome; this has come to be known as the invasion process or the introduction-naturalisation-invasion-continuum (INI Continuum; See **Figure 1.1**). Firstly, a species must be moved via human activity from its native region to an area where it would not naturally have the means to disperse to. Wilson *et al.* (2009) defines six types of dispersal pathways that lead to the movement of alien (syn. non-native, foreign, non-indigenous, exotic) taxa by humans, some of which are intentional and others accidental. In many ways the human-mediated dispersal of alien species, especially when unintentional, shares similarities to natural extra-range dispersal. However, the magnitude at which humans disperse is unprecedented compared to natural disruptions in biogeographic boundaries. In some instances, it is difficult to disentangle the effects of natural versus human-mediated dispersal, especially when they are a secondary consequence of human activity like increased natural disasters as a result of climate change. However, one such dispersal pathway, the *cultivation* of alien species, notably of plants, is uniquely human-mediated and is unlike natural dispersal for a number of reasons: (1) it is often associated with the mass movement and propagation of alien taxa, sometimes to the extent of monocultures; (2) there is often genetic selection of certain traits for utilitarian reasons; and (3) cultivated taxa tend to be nurtured by humans to increase the likelihood of establishment. Hereafter, we will focus on the intentional introduction of plants for cultivation.

A majority of introductions fail, in that the introduced population do not survive simply due to unfavourable environmental conditions or events. However, certain types of human activity can increase the likelihood of introduced populations establishing and this is often especially true for cultivated plants. For example, plants may be introduced and planted in large volumes (e.g. increased propagule pressure) often seen in agriculture and forestry. Certain desirable traits are often selected for, such as propagules that are more robust. And planted populations may be 'fostered' by making the environment more suitable, via irrigation, fertilizer etc.

If alien species are able to establish a self-sustaining population, or naturalise, populations can either simply exist with little consequence, or reproduce and spread beyond the site of

introduction, thus, becoming 'invasive'. There are two main definitions of an "invasive species"; (1) invasive species are defined by their impacts, specifically they are alien species that "become established in natural or semi- natural ecosystems or habitats, is an agent of change, and threatens native biological diversity" (IUCN 1999); (2) The second definition concerns the rate of spread of alien species, and not impacts – According to Richardson *et al.* (2011) for alien plants (the focus of this dissertation), invasive species are those that "produce reproductive offspring, often in very large numbers, at considerable distances from parent plants". For clonal plants that is a spread rate greater than 2 m a year, and for plants that spread via seedling that is those that disperse greater than 100 m from parent plants' in less than 50 years. Richardson's definition therefore considers that some species may be alien, and have environmental impacts, yet do not spread rapidly, if at all.

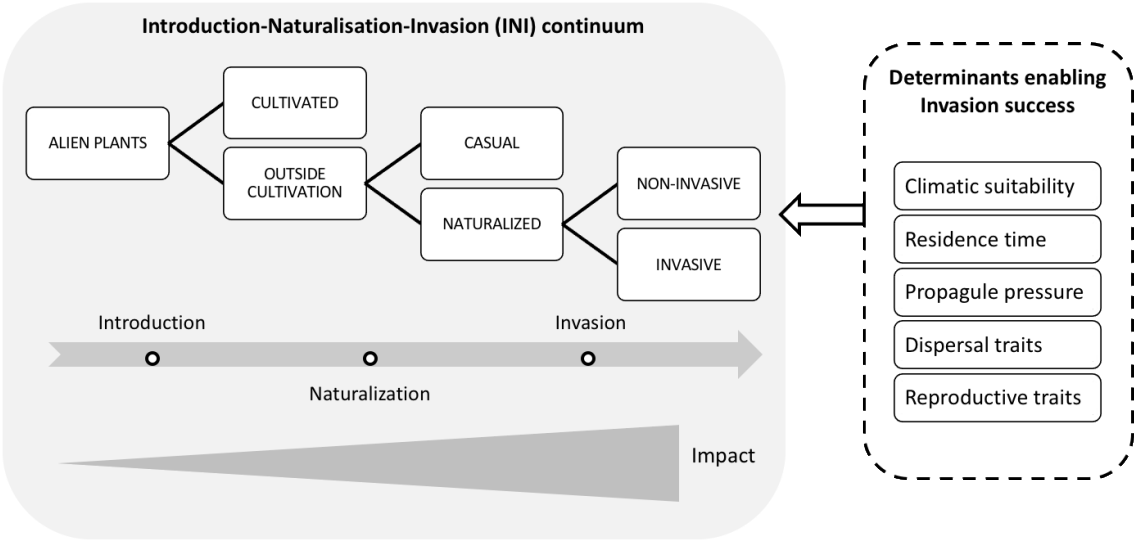

Figure 1.1 The biological invasion process (adapted from Blackburn *et al.* (2011) and Canavan *et al.* (2015)). Introduced taxa must negotiate multiple filters (biological, environmental and human-mediated) to progress along the continuum which is influenced by a number of determinants. The further a population progresses along the continuum the greater the level of impact to receiving ecosystems.

1.1.2 Motivation to introduce alien taxa

There are many reasons why humans intentionally move and cultivate plant species in non-native regions. Here we consider three main drivers: economic reasons, human desirability, and to address environmental problems. Each of these drivers for introduction are compelled by different motivations and target different taxonomic groups. They also have different levels of risk as they select for different traits.

1.1.2.1 Economic introductions

Perhaps unsurprisingly the most extensive intentional introduction of plants has been for economic reasons, namely for agricultural purposes for food security (Smith and Bernatchez 2008). It is estimated that 11% of the world's land surface is under crop production, most of which is with alien taxa that have been genetically selected. (Bruinsma 2017). Agricultural plantings tend to be on a large-scale with a high density of propagules, often planted as a monoculture (Tilman 1999). Food crops are generally not associated with invasions, but land modification and the pathways resulting from agriculture are. For example, there are many weedy species introduced via agricultural hitch-hiker events, such as seeds in animal fodder. Land disturbance from agriculture provides suitable habitats for ruderal weedy species such as those that thrive in fallow fields. Forestry has also been a major pathway of tree introductions for economic purposes. Unlike food crops, tree introductions for forestry are responsible for major woody invasions around the world, especially in the Southern Hemisphere (Richardson and Rejmánek 2011).

1.1.2.2 Introductions driven by human desirability

The introduction of plants for human enjoyment has been compelled for a number of reasons, including the desire to create a landscape for cultural nostalgia, known as the 'Call Home Syndrome' (McNeely 2001). As humans have migrated to new areas they have created familiar environments by planting species from their previous homes. Contrary to this is the 'Allure of the new' where exotic species are sought after for plant collections (McNeely 2001). A good example is the Victorian plant hunters who went to extraordinary lengths to seek rare and unusual species for their collections (Martin 1988, McNeely 2001). Through the pursuit of plants to satisfy human desirability, horticulture ornamental species have been dispersed far and wide. Asia and South America have been major donors of 'exotic' ornamental taxa (Turbelin *et al.* 2017). The horticultural pathway is associated with dispersing the highest percentage of alien species (Turbelin *et al.* 2017). As such, urban gardens have been found to be major launch pads for invasive species into natural areas (Dehnen-Schmutz and Touza 2008, Gaertner *et al.* 2017, Mclean *et al.* 2017).

1.1.2.3 Introductions to address environmental problems

The introduction of alien taxa to address environmental problems is not a new pathway but has certainly seen a considerable rise in interest. In the 20th century it was not uncommon for plants to be introduced to mediate issues with soil erosion, slope stabilisation and deforestation (Milton 2004, Cook and Dias 2006, Bennett 2015). More recently, issues associated with

climate change and environmental degradation are prompting further introductions from new pools of species for a variety of reasons including phytoremediation (filtration of heavy metal and pollutants) and for sources of bioenergy (McIntyre 2003, Richardson and Blanchard 2011, Blanchard *et al.* 2017). Plants that are considered to meet such criteria are often promoted as 'miracle' or 'wonder' crops in that they are plants of current interest that are perceived to offer a service in addressing present environmental problems.

1.1.3 Conflicts of interest

Although many plant introductions are intentional as they are perceived to be useful, not all introduced taxa maintain their value. Further, the perception of how valuable a species is often varies across groups of people, and even between individuals. This introduces the complex topic of 'conflict of interest' – for many species there may have been both benefits and costs associated with alien plants (de Wit *et al.* 2001).

During the early days of European settlement in the Southern Hemisphere there was an extensive exchange of tree species around the world for forestry. Tree species such as Australian acacias (*Acacia* spp.) and mesquite (*Prosopis* spp.) were recognised as a good source of fast-growing woody biomass, stimulating the trade and propagation for economic gain (Griffin *et al.* 2011). However, the combination of weedy attributes, a high degree of propagule pressure and human-mediated distribution of these species facilitated extensive tree invasions (Bennett 2011, Richardson and Rejmánek 2011). These invasions are still prominent in many post-European colonies including South Africa, many of which continue to have a range of impacts (Richardson and Rejmánek 2011). Invasive forestry species demonstrate how, although introduced species may have initial present-day net benefits, the costs associated with management and impacts when species become invasive can superseed the benefits (van Wilgen and Richardson 2014). Further, a change in market preferences (e.g. species lose market value) for certain taxa from changing perceptions can further influence the flux between benefits and costs over time.

It is clear now that the forestry sector has been a major pathway of invasive alien tree species around the world. However, studies on non-timber forestry species have not received as much attention. In the past decade there has been substantial interest in developing commercial plantations of bamboo around the world by forestry organisations. Similar to many tree species certain bamboos are potentially a conflict of interest group in that they can have major environmental impacts in forests and can be an urban nuisance (Canavan *et al.* 2018b). Bamboos

are therefore perceived to be useful and a nuisance by different groups of people. This has raised concerns for the potential of future impacts and invasions of bamboos.

1.2 CASE STUDY: BAMBOOS

This dissertation focusses on the plant group of bamboos to address questions related to human-usage and plant invasions, for the following reasons: (1) they have been a historically useful plant group for humans; (2) they have been widely introduced around the world; (3) they have been introduced for multiple purposes for all three socio-economic pillars including economic use (e.g. for wood, food, forestry), human desirability (e.g. ornamental horticulture), and more recently, for addressing environmental problems (e.g. for phytoremediation, biofuels, soil stabilisation)(Farrelly 1984). Therefore, studying bamboos offers an excellent opportunity to address basic research questions related to facets of invasion science and human activity.

1.2.1 Taxonomy of bamboos

The term "bamboo" is used to refer to all species within the subfamily Bambusoideae in the grass family, Poaceae, which comprises of more than 1,600 species. Bamboos are native to almost every continent with the exception of Europe and Antarctica (**Figure 1.2**) (Kelchner and Bamboo Phylogeny Group 2013). The wide distribution may explain the high degree of diversity among species, with a range extending from cold mountainous regions to tropical areas (Bystriakova *et al.* 2004). The greatest concentration of species is in eastern and southern Asia (Canavan *et al.* 2017b). Mainland Africa has the lowest native richness with only five species, but with the addition of Madagascar the whole African continent has 46 species.

Bamboos can be divided into three main lineages: Arundinarieae (temperate woody bamboos), Bambuseae (tropical woody bamboos) and Olyreae (herbaceous bamboos) (**Table 1.1**) (Kelchner and Bamboo Phylogeny Group 2013). These lineages follow strong geographic divisions. Both woody bamboo lineages make up the 'core group' of bamboos and are defined by a lignified stalk that separates them from most grasses. Herbaceous bamboos have a more questionable affinity to the subfamily and make up only 15% of all species of bamboos (Ohrnberger 1999). This dissertation focusses on woody bamboos because of their extensive usage by humans and also for their invasion potential.

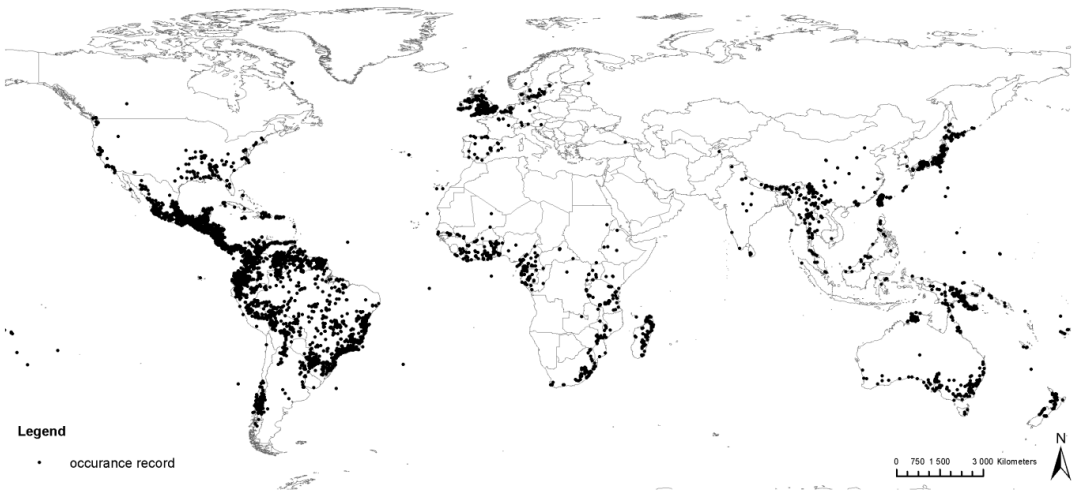

Figure 1.2 The combined native and alien range of bamboos (Poaceae: Bambusoideae). Occurrence data were retrieved from the Global Biodiversity Information Facility (GBIF; https://www.gbif.org).

Table 1.1 Summary of different taxonomic groupings of bamboos, with the number of species and number of genera found in each group across three taxonomic by biogeographic lineage, tribe and subtribe as defined by the Bamboo Phylogeny Group (BPG).

Tribe *(Clark et al. 2015)*	**Number of species**	**Number of genera**
Olyreae	124	22
Bambuseae	812	66
Arundinarieae	546	31
Total	**1482**	**119**

Biogeographic lineage (Kelchner and BPG 2013)	**Number of species**	**Number of genera**
Herbaceous	119	21
Neotropical Woody	413	21
Paleotropical Woody	546	50
Temperate Woody	584	29
	1662	**121**

Tribe or subtribe *(Clark et al. 2015)*	**Number of species**	**Number of genera**
Subtribe Buergersiochloinae	1	1
Subtribe Olyrinae	85	18
Subtribe Parianinae	38	3
Subtribe Arthrostylidiinae	183	15
Subtribe Chusqueinae	172	1
Subtribe Guaduinae	60	5
Subtribe Bambusinae	268	27
Subtribe Hickeliinae	33	8
Subtribe Melocanninae	88	9
Subtribe Bambusinae	812	66
Subtribe Melocanninae	-	-
Subtribe Racemobambosinae	17	1
Tribe Arundinarieae	546	31
	1482	**119**

1.2.2 Social and economic importance

Bamboos feature prominently in Asian history and culture. This can be explained by the natural abundance of native bamboo species, making them an accessible and plentiful resource, with utilization dating back as far as 5000 years in China (Yuming *et al.* 2004). Bamboos are still used as a primary construction material in a similar way wood that is used elsewhere in the world. Some examples of construction with bamboo include large-scale buildings, scaffolding, boats and bridges, to small-scale weaving of baskets, fishing nets, furniture and decorative products (Yuming *et al.* 2004).

Utilization of native bamboos has occurred in other parts of Asia, South America and to a lesser extent Africa. There has also been considerable movement and cultivation of bamboos outside of their native range. About ~50-100 species are routinely cultivated because of their highly valued ornamental and/or agricultural merits (Rao *et al.* 1998), of which, almost half of introduced species come from just seven genera (*Bambusa*, *Phyllostachys*, *Chusquea*, *Fargesia*, *Gigantochloa*, *Dendrocalamus* and *Sasa*; data retrieved from Canavan et al. 2017).

In the past few decades, the global demand for bamboo products has increased (Marsh and Smith 2007, Liese and Köhl 2015, Scheba *et al.* 2017). An upsurge in popularity is partially attributed to an emerging culture surrounding bamboo's potential to provide more sustainable and renewable options compared to current forestry practices (Bansal and Zoolagud 2002). Other reasons include the ability of many species to grow rapidly in marginal soils (some bamboos are among the fastest growing of all plants), coupled with the advent of modern processing techniques for transforming bamboo into many products, thereby enhancing its competitive advantage over traditional timber (Liese and Köhl 2015).

However, due to limitations in land capacity in regions that have historically cultivated bamboo commercially in Asia, they can no longer meet the growing demand for bamboo. As a result, global efforts have been made by inter-governmental organisations such as the International Network for Bamboo and Rattan (INBAR), as well as other global partners to develop plantations in regions that previously did not cultivate or harbour bamboo. In September 2015, INBAR announced a $100 million programme to develop and research a bamboo industry with specific attention to developing economies (Yiping 2015). In particular, focus has turned to countries across Africa as the new bamboo frontier. A notable example has been in South Africa, where a number of pilot projects have started over the last few years.

1.2.2.1 Commercial cultivation of bamboo in South Africa

A bamboo symposium in 2011 in the Eastern Cape was the first sign of developing and commercialising the bamboo industry in South Africa. The symposium was co-hosted by the Eastern Cape Development Corporation (ECDC) and the Industrial Development Corporation (IDC) with the intention of promoting bamboo cultivation.

In a recent study, Scheba *et al.* (2017) sought to document the development of the bamboo industry in South Africa as a means to contribute to the green economy. The study concluded that the bamboo industry is still relatively small-scale. However, there are a diversity of sectors utilising or promoting bamboo. These include nursery/ tissue cultures, commercial growers, specialised retailers, government projects and consultants (**Figure 1.3**). Some examples of on-going projects include: (1) the formation of the National Bamboo Association of South Africa in 2005; (2) Ecoplanet, the world's biggest growers of bamboo outside of Asia, setting up a pilot project in the Eastern Cape with the intention of replicating the success of their development projects in South America; (3) Food and Trees for Africa, an active NGO that has promoted afforestation across South Africa, and has set up a derivative of the company devoted to bamboo plantations "Bamboo for Africa"; and (4) the Beema Bamboo energy project in KwaZulu-Natal, a 500 hectare of land under bamboo experimental cultivation for the purpose of supplying biomass feedstock.

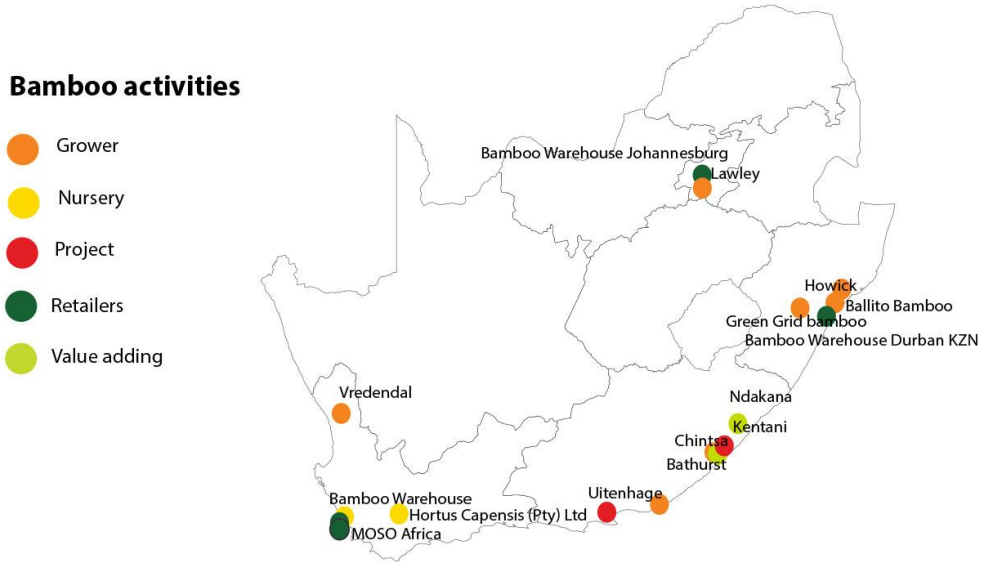

Figure 1.3 Commercial bamboo activities in South Africa (Source: Scheba *et al.* (2017)).

Emerging bamboo projects in South Africa demonstrate how the cultivation of bamboo extends across the private and public sectors with interests from reducing unemployment, uses for carbon mitigation, to alternative "renewable resources". Such bamboo projects could present opportunities for South Africa in terms of foreign investment and developing local industry. However, at this stage there has not been adequate research into the long-term impacts of a large movement that will be fostering alien bamboos en masse. In general, most research on bamboo has focused on agricultural potential, maximising yields and on economic valuation of the industry. Few studies have addressed the environmental risks of propagating non-native species.

1.2.3 Bamboos and invasion science

Experience with past events has shown that although there may be initial benefits to introducing species, there are often long-term impacts that need to be considered. Although bamboos have high economic importance, they also have been associated with invasions and impacts when populations escape cultivation. For example, species belonging to the genus *Phyllostachys* are particularly noted for being noxious weeds in both their native and introduced range (Suzaki and Nakatsubo 2001, Wu *et al.* 2008). They form fast-growing mono-specific stands that displace surrounding vegetation and can be detrimental to local biodiversity (O'Connor *et al.* 2000)(See Chapter 3 for further discussion).

In Japan, plantations of Chinese Moso bamboo, *Phyllostachys edulis*, were established (c. 1730s). However, when the economy moved towards being a service economy over the past century, many agricultural areas including bamboo plantations were transformed or abandoned. With the cessation of management, bamboos spread and have been invading neighbouring land including mixed forests and agricultural plots. Today, the government is actively engaged in managing these invasions. There is a growing body of research on the implication of this event which has had impacts on plant and animal communities, soil composition and hydrology of invaded areas (Kobayashi et al. 1999; Kobayashi & Tada 2010).

1.3 STRUCTURE AND AIMS OF DISSERTATION

This dissertation is presented as a collection of five stand-alone articles (Chapters 2 to 6) that have been published, accepted for publication, or are intended for publication in international journals. It also includes an introductory chapter (Chapter 1), general discussion (Chapter 7) and a consolidated bibliography. All chapters were planned and executed by me. Some chapters have co-authors, where expert advice was needed to complete the chapter, or (in the case of Chapter 4) where the chapter grew from deliberations at a workshop. The contribution of authors is stated at the beginning of each chapter. For the introductory and discussion chapters the first-person singural pronoun "I" is used, but for the article chapters which were written with co-authors the first-person plural pronoun "we" is used. Published papers were formatted so that the dissertation is in a consistent style, but the content was not edited. As a result, there is some repetition, especially in the introduction sections of these chapters. Each chapter contributes towards answering the broader objectives of the dissertation – How does history of usage influence invasion success in cultivated plants? I use bamboos and tall-statured grasses, a highly used and widely distributed group of plants, to explore various questions relating to human-usage from a global perspective to specific case studies in South Africa.

1.3.1 Motivation

The selection of fast-growing plant species for biofuels and other environmental applications in the past decades, in general, has been cause for concern among invasion biologists. Bamboos, and many other tall-statured grasses in particular, have been the focus of many new introduction efforts. While there is certainly an economic case to be made for their introduction, the long-term environmental consequences related to biological invasions of introducing alien taxa has yet to be determined. Given that similar past episodes of promoting 'wonder plants' have led to invasions, there is potential for conflicts of interest to occur in the future, if the risks of future bamboo introductions are not addressed.

A critical part of predicting the threat of new introductions is understanding the outcome of historical introduction events (Seebens, 2018). Bamboos have been an important plant group for humans and therefore particular taxa have had a long history of introduction around the world, with multiple pathways. This makes bamboos an excellent group to study how usage history has influenced current patterns of distribution. However, most studies on bamboo invasions and impacts have been taxon and site specific. Despite their economic importance there has never been a consolidated effort to produce inventories of what species have been moved and what were the outcomes of these movements from an invasion biology perspective. Such a synthesis that would allow one to answer questions like:

1. What were the outcomes of past biogeographic experiments distributing bamboos?
2. Which species have been selected for introduction?
3. Do some bamboos have inherently more invasive traits than others?
4. Do those bamboos that have become invasive simply have traits that make them more desirable to humans and therefore have increased the likelihood of widespread introductions?

1.3.2 Objectives and aims of research chapters

Global scale

Chapter two
Invasion status

Objective:
Review the movement and status of bamboos

Aims:
1. Compile an inventory of all bamboo species and their current global distribution.
2. Determine which species have been introduced and become invasive outside of their native ranges.
3. Explore correlates of introduction and invasion.

Chapter three
Environmental impacts

Objective:
Review the environmental impacts of bamboos

Aim:
1. Compare and score the magnitude and type of impacts of bamboo between the native and non-native range using the EICAT scheme.

Chapter four
Tall-statured grasses

Objective:
Review the usefulness of the tall-statured grasses as a functional group

Aims:
1. Produce and define a list of what constitutes as a of tall-statured grass.
2. Test if there is a quantitative pattern of naturalisation.
3. Identify risks.
4. Discuss the invasion-science literature associated with TSGs.

How does history of usage influence invasion success in cultivated plants?

Case study: South Africa

Chapter five
Socio-historical perspective

Objective:

Understand the history of introduction and current perceptions of bamboos in South Africa

Aims:
1. Present a historical narrative of the introduction of bamboos.
2. Assess the current human perceptions as useful plants and as weeds.

Chapter six
Identification & status

Objective:

Assess the distribution and status of bamboos in South Africa

Aims:
1. Produce an updated inventory of introduced bamboo taxa.
2. Assess the distribution of bamboos from observations and historical records.
3. Determine the invasive status at a key site where there is known high density of bamboos.

2 The global distribution of bamboos: assessing correlates of introduction and invasion

This chapter was published in *AoB Plants*

Canavan, S., D. M. Richardson, V. Visser, J. J. L. Roux, M. S. Vorontsova, and J. R. U. Wilson. 2017. The global distribution of bamboos: assessing correlates of introduction and invasion. *AoB PLANTS*: plw078 doi: 10.1093/aobpla/plw078

Author contributions: S.C, J.R.U.W and D.M.R conceived the idea. S.C compiled the data. V.V. contributed to analysing and visualizing the data for final publication. J.J.L.R. assembled the phylogeny. M.V. provided the GrassBase database. S.C. led the writing of the manuscript with inputs from all co-authors.

2.1 ABSTRACT

There is a long history of species being moved around the world by humans. Introduced species can provide substantial benefits, but they can also have undesirable consequences. We explore the importance of human activities on the processes of species dissemination and potential invasions using the Poaceae subfamily Bambusoideae ('bamboos'), a group that contains taxa that are widely utilised and that are often perceived as weedy. We: (1) compiled an inventory of bamboo species and their current distributions; (2) determined which species have been introduced and become invasive outside their native ranges; and (3) explored correlates of introduction and invasion. Distribution data were collated from Kew's GrassBase, the Global Biodiversity Information Facility and other online herbarium information sources. Our list comprised 1662 species in 121 genera, of which 232 (14 %) have been introduced beyond their native ranges. Twelve (0.7 % of species) were found to be invasive. A non-random selection of bamboos have been introduced and become invasive. Asiatic species in particular have been widely introduced. There was a clear over-representation of introduced species in the genera *Bambusa* and *Phyllostachys* which also contain most of the listed invasive species. The introduction of species also correlated with certain traits: taxa with larger culm dimensions were significantly more likely to have been moved to new areas; and those with many cultivars had a higher rate of dissemination and invasion. It is difficult to determine whether the patterns of introduction and invasion are due simply to differences in propagule pressure, or whether humans have deliberately selected inherently invasive taxa. In general, we suggest that human usage is a stronger driver of introductions and invasions in bamboos than in other taxa that have been well studied. It is likely that as bamboos are used more widely, the number and impact of invasions will increase unless environmental risks are carefully managed.

2.2 INTRODUCTION

Human-mediated dissemination of species has intensified over the past three centuries with the increase of global traffic (Meyerson and Mooney 2007, Ricciardi 2007). Some introduced species naturalize (reproduce consistently) in their new ranges and some naturalized species invade (spread from sites of introduction). This has created a global-scale natural experiment in biogeography (Bardsley and Edwards-Jones 2006, Richardson 2006, Yoshida *et al.* 2007, Richardson and Blanchard 2011, Richardson and Rejmánek 2011). Considerable efforts have been made by invasion scientists to understand the key drivers of invasion, and to determine whether generalisations can be made on how some species manage to overcome barriers associated with different stages of the introduction-naturalization-invasion continuum (Blackburn *et al.* 2011, Richardson and Pyšek 2012, Kueffer *et al.* 2013, Moodley *et al.* 2013). However, as introduced taxa often represents a non-random selection of all taxa, there is some 'taxonomic selectivity' in which taxa become invasive (McKinney and Lockwood 1999).

Biological invasions are, by definition, the result of human-mediated dispersal and can only be understood in the context of human activities. The movement of species is often influenced by their direct value to humans (McKinney and Lockwood 1999), in particular as introduced species have been essential to the development of all contemporary human societies (Prance and Nesbitt 2005). With intentional plant introductions, morphological traits have been shown to be important in facilitating the introduction and invasion of species (Pyšek and Richardson 2008). Certain traits may be of high value to humans at the introduction stage and thus influence the initial movement of these species into new ranges. For example, Proteaceae with showy flowers and Cactaceae with other traits valued for ornamentation were found to be overrepresented among introduced species in these families (Moodley *et al.* 2013, Novoa *et al.* 2015). For both these families, traits that enabled greater ability to spread were found to be more important for invasion success post-introduction. Traits underlying invasion success can also be highly taxon or context specific. In many woody plant taxa, such as *Acacia*, *Pinus* and Proteaceae, seedbank size and longevity are associated with invasion success (Grotkopp *et al.* 2002, Richardson and Kluge 2008, Moodley *et al.* 2013), while in Cactaceae growth form is an important determinant of invasion success (Novoa *et al.* 2015).

We focused on bamboos, a large subfamily of the grasses (Poaceae: Bambusoideae; 1662 species in 121 genera). Bamboos have a range of functional forms distributed over numerous biogeographic regions, including dwarf herbaceous species found in temperate climates and giant tropical woody species that can grow up to 20 m tall (Bystriakova *et al.* 2004). It is

estimated that 2.5 billion people are directly involved with the production and consumption of bamboo (Scurlock *et al.* 2000). The main economic value of bamboo lies in the utility of the hardened culm, which serves many of the same functions as timber (Scurlock *et al.* 2000, Chung and Yu 2002). What makes bamboo a particularly interesting group beyond timber functions, however, is the versatility of uses and the utilisation of all plant parts. Leaves are used for fodder, shoots for human consumption, culms for biomass, construction, textiles, musical instruments and many bamboos are used in horticulture (Hunter 2003). This has led to many species being intentionally moved outside of their native ranges (Cook and Dias 2006, Townsend 2013).

Over the past few decades, bamboos have seen an upsurge in popularity, largely driven by a perception of certain species as wonder plants or miracle crops, i.e. plants that are believed to be especially valuable in meeting current economic, environmental and social needs (Hoogendoorn and Benton 2014, Liese and Köhl 2015). Various authors have argued that commercially grown bamboos are more sustainable and renewable than current forestry crops (Bansal and Zoolagud 2002, Song *et al.* 2011). Modern processing techniques have also transformed the range of products that can be made from bamboo. Therefore, the rate at which species are being introduced and cultivated in new ranges has increased; especially cultivation of bamboos in response to an increased global demand for timber products (Hunter 2003, INBAR 2003).
Most research on bamboos has focused on aspects of commercial cultivation and uses such as methods for maximizing yields and on providing economic valuations of plantings in different contexts. To date, we are not aware of any comprehensive studies on the invasion ecology of bamboos, despite their reputation for being a group that contains highly 'invasive' species (Space and Flynn 1999, Buckingham *et al.* 2011). Many species possess weedy attributes, such as fast growth rates, clonal reproduction and the formation of long-lived monospecific stands (Lima *et al.* 2012). Bamboos can dramatically alter ecosystem dynamics through competitive exclusion and expansion of patches that form from clonal reproduction**.** A growing number of papers address some of these issues (Blundell *et al.* 2003, Kudo *et al.* 2011, Lima *et al.* 2012, Kobayashi *et al.* 2015, Suzuki 2015, Yang *et al.* 2015, Rother *et al.* 2016).

While there has been a long history of bamboo introductions, little is known about which species have been moved where, and the outcomes of these movements. The aims of this paper were to (1) compile an inventory of all bamboo species and their current global distribution; (2) determine which species have been introduced and which have become invasive outside of their native ranges; and (3) explore correlates of introduction and invasion. We expected that certain

correlates, both biological (i.e. taxonomy, phylogeny, plant traits) and social (i.e. introduction effort, the utility of species), will have resulted in taxonomic selectivity in introduction effort (**Table** 2.1).

Table 2.1 Features correlated with the introduction and invasion status of bamboos.

Correlate/ Measurement	Expectation	Result	Consequence	Figure/Table in this paper
Taxonomy (genera)	Introduced species will tend to come from certain genera.	The genera *Bambusa*, *Semiarundinaria*, *Shibataea*, *Phyllostachys*, and *Thyrsostachys* had a significant proportion of species that have been introduced. *Bambusa*, *Phyllostachys* and *Pleioblastus* had a significant proportion of species that were invasive relative to other genera.	The pool of introduced species is a very particular subset of all bamboos, so need to be careful about assessing traits linked to invasiveness only on introduced taxa.	**Figure 2.4**
Phylogeny	There will be a non-random assortment of which species are introduced across the phylogeny.	Only culm height showed significant phylogenetic signal, other variables including status were not significant.		**Appendices**
Lineage (Neotropical woody etc.)	Taxa from particular biogeographical regions are more likely to become introduced (even if phylogeny and introduction history are taken into account).	Temperate bamboos have had a high rate of species introduced compared to other lineages. Both temperate and Paleotropical woody bamboos contain invasive species, but neither had a significant number compared to the other.	Bamboos from other parts of the world are likely to have significant potential for utilisation in the future. Region of origin could be an important correlate of risk.	**Table 2.2**
Number of countries / regions a species have been introduced to	Species of bamboo that have been introduced to many ranges will have a higher likelihood of becoming invasive.	The number of countries a species has been introduced to was strongly (positively) correlated with the likelihood of it being invasive.	Risk and impacts caused by non-native bamboos are a function of propagule pressure	-
Number of cultivars	Species with a greater number of cultivars will be more likely to have been introduced than species with fewer cultivars.	Introduced species tended to have more cultivars.	There has been a possible selection for species that show high levels of phenotypic variation, this can potentially be linked to a greater ability to adapt and so become invasive. On the other hand, more efforts may have simply been made to develop cultivars for common species.	-
	Species with many cultivars will have a higher likelihood of becoming invasive.	Greater number of cultivars was an important determinant of invasion.	Invasiveness has been selected for during breeding and cultivation practices.	

Culm form	Woody lineages will have a higher proportion of introduced species than herbaceous.	Woody bamboos are preferred for introduction.	As herbaceous species have had much lower rates of introduction, there has been a bias in the natural experiment.	**Table 2.2**
Culm dimensions (diameter and height)	Introduced species will on average have greater culm dimensions than non-introduced species.	There is an affinity for species to be introduced that have greater culm dimensions.	Smaller bamboos will be less likely to have been introduced.	**Figure 2.5**
Rhizome form (running or clumping species)	Introduced bamboo species with running rhizomes are more likely to become invasive, although there is no prior expectation as to how this might affect which species are introduced.	Rhizome form was not an indicator of invasive species. However we did find more running type bamboos have been introduced (although this is correlated with temperate species which have had a bias for introduction).	Control and regulation of bamboos should consider both running and clumping forms.	**Table 2.2**

2.3 METHODS

2.3.1 Inventory of species and distribution

Establishing inventories of taxa, their distribution and cases of invasions are fundamentally important in the field of invasion science and the lack of such information can hinder management efforts (McGeoch *et al.* 2012). To document the dissemination of bamboos, we required up-to-date taxonomic lists and distribution data.

The identification of bamboos is notoriously problematic (reviewed by Kellogg (2015)). Due to the rarity of flowering cycles (7 to more than 120 years in woody species; Janzen (1976)), species identification often relies heavily on vegetative material, but most species have few, if any, reliable diagnostic vegetative features. Consequently, there are major discrepancies between the classification of bamboos and species lists. Significant improvements have been made by specialist groups such as the Bamboo Phylogeny Group (2012) and, more generally, by GrassBase, an on-going international initiative to collate taxonomic data on the family Poaceae at the Royal Botanical Gardens, Kew, UK. GrassBase includes a list of all bamboo species, their distributions and trait data (Clayton *et al.* 2015, Vorontsova *et al.* 2015). We verified and updated the accepted taxa in GrassBase both as one of us has specialist experience in grass taxonomy (MSV) and by collaborating with a bamboo taxonomy specialist (Lynn G. Clark, Iowa State University). We also included recent literature on new species and other changes in classification published up to September 2015 (Kellogg 2015) [see Supplementary Material—for full species list].

An extensive search was undertaken between June 2014 and January 2015 to document the introduction of bamboos to areas outside of their native ranges. This included searches of the Web of Science and other platforms of academic and grey literature. Most information was retrieved from online databases specialising in global herbarium records and/or non-native species records, namely the Global Biodiversity Information Facility (GBIF), Kew's GrassBase, the Global Compendium of Weeds (GCW), Pacific Island Ecosystems at Risk (PIER), Delivering Alien Invasive Species Inventories for Europe (DAISIE), Invasive Species Specialist Group (ISSG) and CABI's Invasive Species Compendium (CABI-ISC), but independent literature searches also provided useful data. GBIF provided the greatest amount of data on the locality of species with over 84 000 entries for 'Bambusoideae' species. Of these, around 29 %

of records had sufficient ancillary data for our purposes (of the 71% that did not, 8 % lacked a scientific name, 21 % a country and 71 % a locality)

When pooled with the other databases, 179 species names did not match our accepted species list. Unknown names were removed; synonyms and spelling errors were updated or corrected accordingly and kept in the final database [see Supplementary Material]. We discarded records on the basis of names that we could not resolve using these criteria. The final list for analyses included over 27 000 entries. Names of geographic regions were defined based on the International Organization for Standardization for country codes and regions (ISO 31661-1 standard; with the exception of a few island regions which were independently defined, such as Hawaii and the Galapagos Islands).

2.3.2 Dissemination and status

We categorized the presence of a species in a given country or region as native or non-native (or introduced) based on distribution data from Kew's GrassBase and cross-referenced with Ohrnberger (1999). These two data sources provide a complete inventory of the taxonomy and distribution of bamboos that was needed to establish native and introduced ranges. We defined these categories using the compendium of concepts in invasion science proposed by Richardson *et al.* (2011). Species were listed as 'non-native' or 'introduced' when their presence in a region is due to human activity. Note that our records do not distinguish between successful introductions (where species have been established and are still present today) and failed introductions (where species no longer occur in that region)—they simply reflect the presence of a species in a given region at some point in time. We classified a subset of 'non-native' species as 'invasive'. Invasive species are 'naturalized plants that produce reproductive offspring often in large numbers at a considerable distance from parent plants…' (Richardson *et al.* 2011). Records of bamboos being listed as invasive were found either through the databases mentioned above, or through an independent literature search. References for invasions came from a combination of peer-reviewed literature and official government reports, which were then cross-checked to validate claims that species were 'invasive' following the criteria of Richardson *et al.* (2011) [Supplementary Material].

To conceptualize and display the flows of introduced and invasive species between and within different biogeographic regions around the world, we used circos visualization from the R package 'circlize' (Gu *et al.* 2014).

2.3.3 Correlates of introduction and invasion

2.3.3.1 Morphological traits

To determine whether particular traits were related with the introduction status and invasion success of bamboos, we collated trait data from GrassBase. The dataset included 14 trait categories (culms, culm-sheaths, leaves, ligule, etc.). However, only culm dimensions (diameter and height) and underground rhizome system (runner or clumper) were consistently recorded (data on other traits were not available for more than half of the species). These traits were chosen as they were considered relevant to the study and data were available for many of the species.

Different culm properties provide different benefits—thicker-walled culms yield more biomass, greater diameter can produce stronger culms, etc. (Scurlock *et al.* 2000, Chung and Yu 2002). To determine whether introduced and/or invasive species had taller and/or wider culms than non-introduced species, we used linear models with log-transformed culm dimension (height or diameter) as a response variable and introduction status as the predictor variable. We also included lineage affiliation (paleotropical woody, neotropical woody, temperate woody and herbaceous) as an additional predictor as these have been identified as genetically distinct groups within bamboos that have particular growth forms associated with each (Kelchner and Bamboo Phylogeny Group 2013). We also tested the differences in culm form of woody versus herbaceous groups in a number of introduced species compared with non-introduced species, and the number of invasive compared with non-invasive species using Fisher's exact tests. All statistical tests were conducted in R (R Core Team 2015).

Underground rhizome type was also considered a relevant trait for invasion success, as it is often used as a means of separating invasive from non-invasive bamboos (Hamilton 2010; Royal Horticultural Society 2015). There are two forms: running (leptomorph) and clumping (pachymorph). Although sub-forms exist within these categories, for simplicity we only used these two broad categories. Running species are considered to have a greater ability to spread rapidly and are generally considered more invasive than clumping species (Buckingham *et al.* 2014). To test the difference in number of running and clumping species in the groups of introduced compared with non-introduced, and the number of invasive compared with non-invasive species, we used Fisher's exact tests.

2.3.3.2 Taxonomic, geographic and phylogenetic patterns

The exchange of species and the rates of invasion are rarely random, but often have distinct patterns that are influenced by a number of factors, some human-mediated and others related to the evolutionary history of species. Within particular groups this can lead to ′taxonomic selectivity′. In the case of bamboo, forestry and horticulture have been the main drivers of introductions, and this has led to the preferential selection of taxa. To test whether introductions and invasions have been random, we used Fisher's exact test to analyse differences between numbers of introduced compared with non-introduced species, and the number of invasive compared with non-invasive species across genera, lineages (i.e. neotropical woody), and introduced countries.

If certain bamboo traits are important to invasion success, and if these traits reflect evolutionary history, then we would expect the phylogeny to indicate ′taxonomic selectivity′, with only certain lineages becoming invasive. Much work has been done on reviewing this phenomenon to improve the prediction of extinctions. Studies have found that extinctions within taxonomic groups in birds, mammals and plants tend not to be randomly distributed across phylogenies but are concentrated in particular high-risk clades (McKinney and Lockwood 1999, Fritz and Purvis 2010). This is arguably due to phylogenetically conserved life-history traits or ecology (Schwartz and Simberloff 2001, Purvis 2008, Fritz and Purvis 2010). There is evidence to suggest this is also true with invasiveness across taxa (McKinney and Lockwood 1999, Lockwood *et al.* 2001, Novoa *et al.* 2015, Yessoufou *et al.* 2016). We explore this for bamboos by testing the phylogenetic signal of status (introduced/invasive) and other correlates of introduction and invasion. To do this we collated genetic data for one chloroplast gene region (maturase K; *matK*) for all taxa with available data in the online GenBank repository (ncbi.nlm.nih.gov) for phylogeny reconstruction. Where possible, GenBank accessions denoted as 'voucher' specimens were used. Our final dataset comprised 124 taxa (including two non-bamboo grass species *Bromus interruptus* & *Trisetum spicatum* as outgroup taxa). DNA sequence data were combined and aligned in the BioEdit version 7.0.5.3 and were edited manually (Hall 2006). Flanking regions were trimmed to avoid excessive missing data. Our final DNA alignment consisted of 860 characters and contained three gaps ranging between 1 and 6 base pairs. A Bayesian inference phylogeny was reconstructed using Mr Bayes v 3.2 (Ronquist and Huelsenbeck 2003). jModelTestv2.13 (Darriba *et al.* 2012) and the Akaike information criterion (Akaike 1973) determined the best fit model for our data as the GTR + I +G model. The Bayesian model was run for 1.5 million generations sampling every 1000th generation and a consensus tree was built, discarding the first 25 % of trees as burn-in.

Posterior probabilities (PP) were calculated using a majority rule consensus method to assess tree topology support.

To test whether continuous traits (culm dimensions) are phylogenetically clustered or over-dispersed, we used Blomberg's K statistic with a null hypothesis of Brownian Motion Model (Blomberg *et al.* 2003). We also tested for phylogenetic signal of other variables, i.e. introduction and invasion frequency (the number of countries a species has been introduced to or become invasive), and propagule pressure (using the frequency of cultivars as a proxy; see below) using Pagel's λ (lambda) which uses transformation of the branch lengths assuming Brownian motion (Pagel 1999). Both analyses were done using the R packages 'phytools' and function Phylosig.R (Revell 2012). Species traits, status and cultivar diversity per species were mapped onto the phylogeny to visualise patterns using the R package 'adephylo' (Jombart *et al.* 2010) [Supplementary Material]. We used the ***D*** statistic (Fritz and Purvis 2010) to test for phylogenetic signal and strength of binary traits. This method tests whether traits are randomly assigned across the phylogeny tips (when ***D*** equals 0), and whether they are clustered (***D*** equals 1) under a Brownian threshold model. We carried out two tests: one for introduction status (introduced/not introduced) across the whole phylogeny; in the second, we used a tree trimmed to include only introduced bamboos and tested invasion status (invasive/not invasive). This was done using the R package Caper with function phylo.d (Orme 2013).

2.3.3.3 Introduction effort and utility

Many species of bamboo have had cultivars developed for improving their utility and value. We suggest that cultivar diversity associated with species could provide a proxy and quantitative means to measure their popularity and utility. Cultivars are cultivated plant varieties that are developed through selective breeding, genetic manipulations such as polyploidization and hybridization. They are often distinctive, uniform and stable and retain key characteristics when propagated (Brickell *et al.* 2009). Cultivar diversity likely corresponds with propagation frequency and will, therefore, be an important determinant of the probability of introduction, as well as invasion success.

As there is no officially accredited list of bamboo cultivars, we used the list compiled by Ohrnberger (1999) based on the 1995 International Code of Nomenclature for Cultivated Plants (ICNCP). To assess the relationship between introduction status and the number of cultivars developed we used a generalized linear model with a Poisson error structure with

number of cultivars as the response variable and status as a predictor variable. As a proxy of introduction effort, we used the number of regions into which a species has been introduced. We tested for this using a generalized linear model with a Poisson error structure with the number of regions a species has been introduced to as a predictor variable and the number of regions a species is invasive in as a response variable.

2.4 RESULTS

2.4.1 Inventory of species and distribution

Our final list of bamboo species contained 1662 species representing 121 genera, with native species distributed across 122 countries and distinct islands/regions.

2.4.2 Dissemination and status

Two hundred and thirty-two species (14 % of the species in the subfamily) are known to have been introduced outside of their native ranges, with about 5.2 % (12 species) of these introduced species becoming invasive (**Figure 2.1**). However, some regions of the world were markedly over- or under-represented in terms of the number of introduced species (**Figure 2.2**). There were also cases of unknown or disputed native ranges possibly due to a combination of a high degree of introductions and/or lack of reliable records (11 species across 60 countries and regions)**.** Asiatic species have been most widely exported, with Oceania, North America and Europe being the predominant recipients (**Figure 2.1**). All the species reported as invasive are Asiatic. Although South America has a rich native bamboo flora, most movements of these species have been within the continent. We found no evidence of invasive alien bamboos originating from this region. The range of invasive species is shown in **Figure 2.3**.

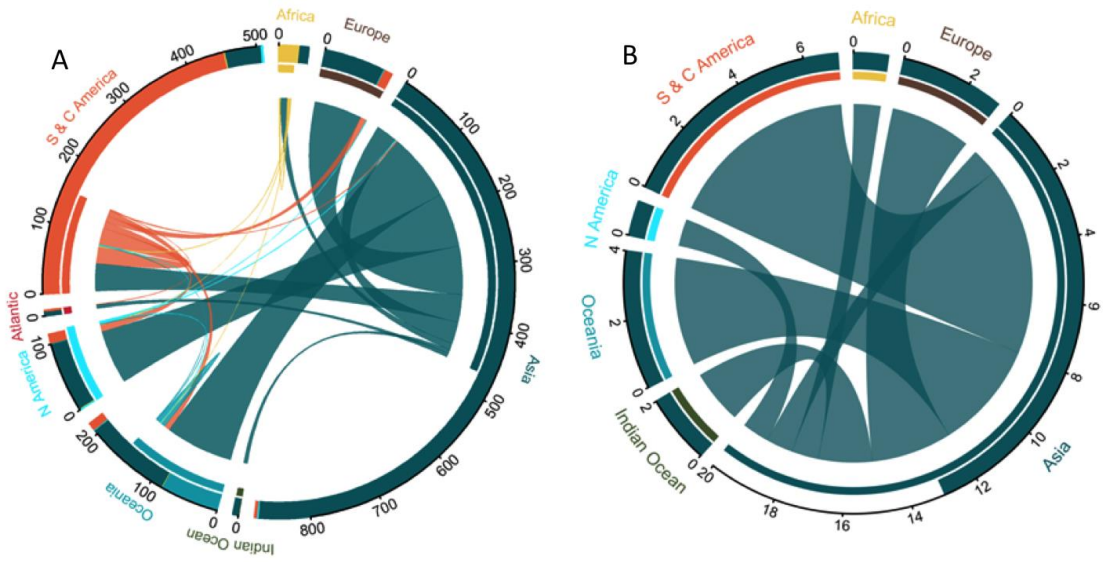

Figure 2.1. Connectivity plots indicating the transfer of (A) introduced species and (B) invasive species of bamboos around the world relative to their native region. The thickness of internal lines connecting regions correspond to the diversity (number) of species moved. The outer inset bar graph shows the total count of species in that region (by status), and the inner bar graph represents the flow to and from that region. Regions are colour coded by label names.

2.4.3 Correlates of introduction and invasion

2.4.3.1 Morphological traits

We found all three trait characteristics tested (rhizome form, culm height and culm diameter) to be significantly associated with different stages along the introduction-naturalization-invasion continuum. For rhizome forms, a significantly higher proportion of introduced species had runner rhizomes (leptomorphs) than clumping rhizomes (pachymorphs), but there was no significant difference in rhizome form for invasive species (**Table 2.2**).

For culm dimensions, there were significant differences between lineages ($F(3,791) = 89.65$; $P < 0.001$); we, therefore, included lineage affiliation in the analyses below. We found that the average culm diameter for introduced bamboos was significantly greater than for non-introduced bamboos ($R^2 = 0.2687$, $F(5,786) = 57.75$, $P < 0.001$). There was no significant difference in diameter between introduced and invasive species of bamboos in general. Within the paleotropical woody group, species were found to have wider culms relative to other groups. Culm height was greater in the group of introduced species ($P < 0.001$) and for the invasive group ($P = 0.015$), compared with the non-introduced group of species. All woody groups were

found to be significantly taller than the herbaceous group ($R^2 = 0.5039$, $F(5, 937) = 190.4$, $P < 0.001$).

Table 2.2 The effect of biogeographic lineage, culm form and underground rhizome form on whether taxa tended to be introduced or become invasive. Each group was tested independently to determine whether species in a particular group or with particular features have been introduced and become invasive significantly more often than other bamboo species. This was done using a Fisher's exact test comparing the number of introduced versus non-introduced species, and invasive versus non-invasive.

	All	**Status**					
		Introduced			Invasive		
	N	N	%	P	N	%	P
Biogeographic lineage							
Temperate woody	500	**101**	**20.2 (16.8-24.0)**	**0.0067**	**8**	**2 (0.9-3.8)**	**0.022**
Paleotropical woody	450	**72**	**16.0 (12.7-19.7)**	**0.0088**	4	1 (0.3-2.7)	1.00
Neotropical woody	300	32	11.0 (7.9-15.0)	0.813	**0**	**-**	**0.0460**
Herbaceous	114	**8**	**7.0 (3.1-13.4)**	**0.0005**	0	-	0.615
Culm form							
Woody	1293	**202**	**16.4 (14.4-18.5)**	**0.0067**	12	1.1 (0.6-1.9)	0.615
Herbaceous	114	**7**	**7.0 (3.1-13.4)**	**0.0067**	0	-	0.615
Underground rhizome form							
Running	331	**71**	**21.4 (16.9–26.4)**	**0.0018**	8	1.6 (0.4–4.1)	0.24
Clumping	860	**116**	**13.5 (11.2–16.0)**	**0.0018**	4	0.7 (0.2–1.6)	0.24

2.4.3.2 Taxonomic, geographic and phylogenetic patterns

At the lineage level, temperate and paleotropical woody bamboo species have been introduced to significantly more countries/regions compared with other groups (**Table 2.2**). Herbaceous species had a low proportion of introduced species. Both temperate and paleotropical woody bamboos contained invasive species, yet only temperate woody taxa had a significant proportion of introduced species that have become invasive. At the genus level, there was a

significantly (Fisher's exact test; $P < 0.05$) high proportion of introduced species that belonged to the genera *Arundinaria* (100 %), *Thyrostachys* (100 %), *Semiarundinaria* (71.4 %), *Phyllostachys* (63 %), *Shibateae* (57.1 %), *Himalayacalamus*(50 %) and *Bambusa* (25.6 %) (**Figure** 2.4).*Phyllostachys* ($n = 5$) and *Pseudosasa* ($n = 2$) were significant in the number of invasive species, with the remaining invasive species belonging to *Bambusa* ($n = 3$), *Dendrocalamus* ($n = 1$) and *Pleioblastus* ($n = 1$).

With respect to phylogenetic signal, our retrieved phylogeny showed low resolution due to the conservative nature of the *matK* gene. Nevertheless, major and well-supported clades corresponded well with higher-level bamboo taxonomy (e.g. subtribe) and known biogeography. Of the continuous traits tested, culm height ($K = 0.097$, $P = 0.014$) had a significant phylogenetic signal using Blomberg's K statistic; but using Pagel's λ both culm height ($\lambda = 0.251$, $P < 0.001$) and culm diameter ($\lambda = 0.418$, $P < 0.001$) were significant. For our binary status traits, we found a random pattern for introduction status ($D = 0.96$, $p_{rand} = 0.273$, $P_{BM} = 0.00$) and for invasion status ($D = 1.24$, $p_{rand} = 0.77$, $P_{BM} = 0.00$).

2.4.3.3 Introduction effort and utility

We found strong evidence that cultivar diversity was associated with introduction status. Species with more cultivars were significantly more likely to have been introduced ($b = 3.56 \pm 0.277$, $P < 0.001$) and have become invasive ($b = 5.89 \pm 0.313$, $P < 0.001$). Compared with introduced species, invasive species had a greater number of cultivars ($b = 2.32 \pm 0.181$, $P < 0.001$), and non-introduced species had significantly fewer cultivars ($b = -3.56 \pm 0.298$, $P < 0.001$). Furthermore, we found that the number of regions a species was invasive to, to be positively and significantly correlated with the number of regions to which a species has been introduced (Poisson GLM: $b = 1.02 \pm 0.090$, $P < 0.001$).

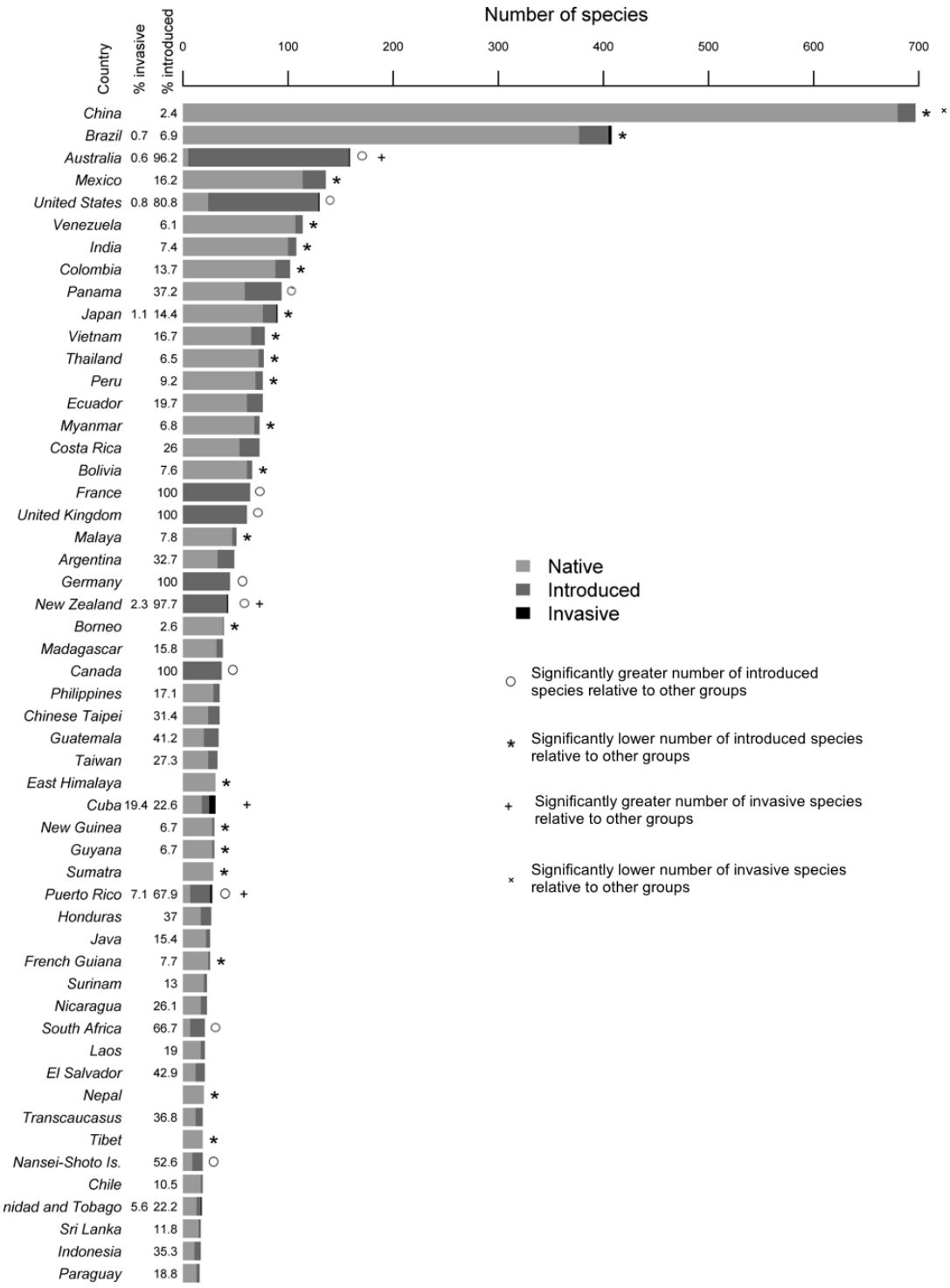

Figure 2.2 Number of bamboo species found in 52 countries and islands with the highest bamboo richness. Regions with less than 15 species were excluded (135 regions) from the figure. Shading indicates the status of bamboo species in that region (native/introduced/invasive). Significance was calculated using Fisher's exact tests between numbers of introduced compared with non-introduced species and numbers of invasive compared with non-introduced species across countries.

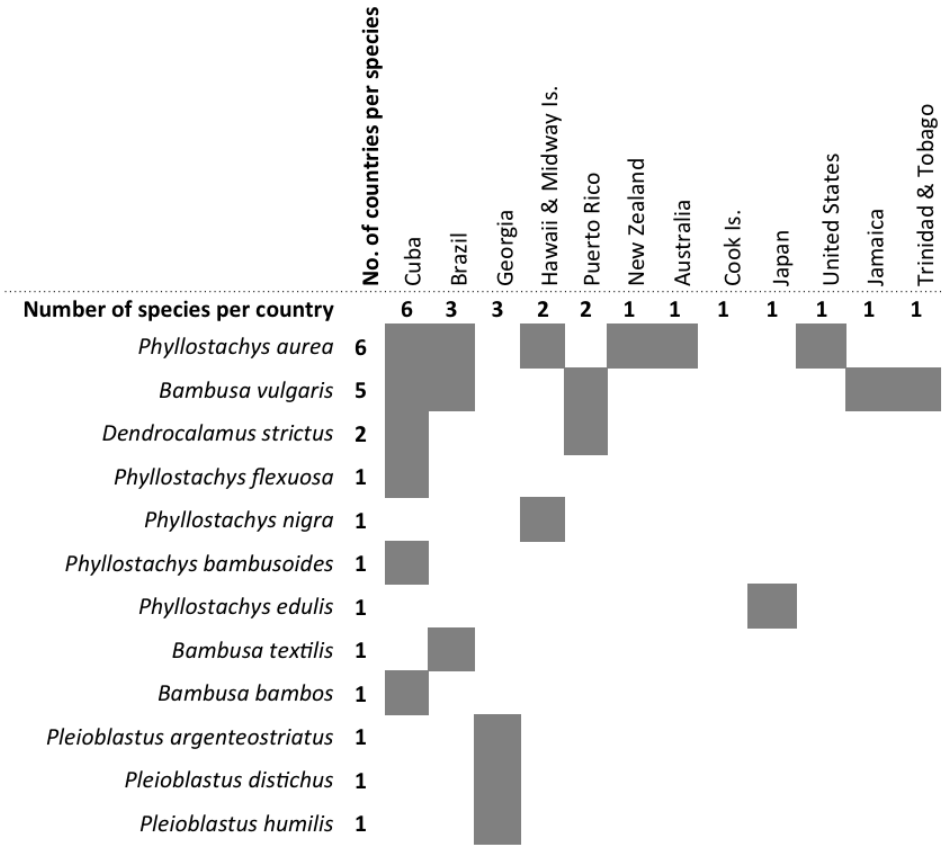

Figure 2.3 Summary of invasive bamboos species and associated region of invasion.

2.5 DISCUSSION

Bamboo species have had a long history of introductions and are now commonly found around the world (**Figure 2.2A** and **Figure 2.2**) but only a few (12) species are invasive (**Figure 2.3**). As predicted, the movement of bamboos is, however, far from complete and the selection and distribution of species has not been random. We identified three main factors that appear to have influenced patterns of introduction and invasion: introduction effort, propagation of species and selection of traits. Each of these is discussed below and we conclude with an assessment of the current extent of bamboo invasion and expansion of some taxa in their native ranges.

2.5.1 Introduction effort

Introduction effort, or propagule pressure, has consistently been linked with successful invasions as greater numbers of propagules and more frequent introductions mean higher probabilities of invasion (Lockwood *et al.* 2005, Von Holle and Simberloff 2005, Colautti and Lau 2015). The positive correlation of propagule pressure and invasion success has been observed in many taxa including birds (Veltman *et al.* 1996, Duncan 1997), mammals (Crowell 1973, Forsyth *et al.* 2004) and aquatic species (Colautti 2005, Duggan *et al.* 2006). This is notable with intentional introductions, such as the case with many ornamental (Dehnen-Schmutz and Touza 2008) and cultivated agricultural (Pyšek and Richardson 2006) plants. We found a clear link between introduction effort and invasiveness in bamboos. Although it was not possible to measure propagule pressure directly, species that had been more widely disseminated were much more likely to have become invasive.

Historical activities in the native range have also played an important role in influencing introduction effort. For example, the local propagation and use of native species may increase the chance of a species becoming established after introductions (Forcella and Wood 1984, Lockwood *et al.* 2005, Pyšek *et al.* 2008). Woody bamboos, in particular, have long been used as a harvested forest resource in regions where they are native (Lobovikov *et al.* 2007). We found that woody bamboos from Asia have been introduced much more often than species from other regions, and all invasive bamboos are native to Asia. This may be explained by an extensive history of active cultivation of woody bamboos around the continent which has promoted the movement of a subset of species (Scurlock *et al.* 2000, Yuming *et al.* 2004, Yuming and Chaomao 2010). Notably in China, bamboo has been widely used for millennia (Li

and Kobayashi 2004). Bamboos have shaped the history of this region and they are now an ingrained cultural and economic aspect of many Asian societies. This would have profoundly influenced the way bamboos from this region have been distributed to other parts of the world.

By comparison, the exploitation of bamboo resources in South and Central America, regions also rich in native bamboo species (roughly 32 % species; 530 species), has been historically limited to local and small-scale usage as a forest resource, and, to a lesser extent, as a cultivated crop (Londoño 1998). The number of exported species (or propagation with regards to cultivars) has been low compared with Asiatic species, with the movements being mostly within the continent (**Figure 2.1A**). If these patterns continue, it is likely that future introductions will continue to come from Asia, although there might be significant untapped potential in bamboos from the Americas (Li and Kobayashi 2004).

We found strong selection bias, and, therefore, taxonomic selectivity, for the mostly Asian genera *Bambusa* and *Phyllostachys*. Both genera harbour a high number of invasive species (relative to other bamboo genera) and have been extensively introduced around the world (**Figure** 2.4). *Phyllostachys* is a highly utilized temperate woody genus (59 species) from Asia, mostly central China. More than 50 % of species in this genus have been moved outside of their native ranges (the highest proportion of any bamboo genus), and six species are listed as invasive. *Bambusa*, a paleotropical woody genus, is also highly utilized and is the second largest bamboo genus (149 species). At least 25 % of species in the genus have been introduced to areas outside their natural ranges, and three species have become invasive. Of these, *B. vulgaris* is the most widely distributed species (123 countries); indeed it deserves the title of 'the most common bamboo in the world' (Farrelly 1984). The introduction of *B. vulgaris* to many tropical islands in the Pacific and the Caribbean by early shipping trade routes has left a legacy of naturalized populations (Rashford 1995, O'Connor *et al.* 2000).

2.5.2 Propagation of species

The fact that some bamboo taxa have been introduced much more widely than others is similar to the patterns observed in other plant groups where there has been a clear bias for species with traits associated with human-usage (Moodley *et al.* 2013, Novoa *et al.* 2015). Species suited for ornamental and agricultural purposes have a higher degree of introduction effort. The horticulture trade in particular has been consistently identified as a major introduction pathway for invasive plants (Dehnen-Schmutz and Touza 2008). Aspects of the industry have been found to be good indicators of risk. For example, increased market availability of species and lower

prices of seeds were found to increase the invasion success of species traded in the British horticultural market (Dehnen-Schmutz and Touza 2008).

Drew *et al.* (2010) argued that the horticultural industry is driven by a demand for novel and exotic species, but that there is also a demand for more robust (i.e. with higher stress tolerance) plants for easy maintenance. As the development of cultivars has helped the industry meet some of these demands, cultivar diversity likely reflects the utility (and market demand) of species for horticulture or cultivation. In the case of bamboos, where there has been a consistent and long history of propagation and distribution of plants for horticulture (ornamental plants, landscape improvement, erosion control, etc.) and agroforestry (construction material, crafts, paper pulp, fuel), we expected that the movement of bamboos would be partially influenced by popularity of certain species (Rashford 1995, Lobovikov *et al.* 2007). We found that greater cultivar diversity of species was strongly correlated with the frequency of introductions, and even more so with invasions. We also noted that our list of cultivars were all species of Asian origin, providing further support for the view that historical cultivation of species in this region has been a key determinant for their global export.

Although we did not measure the market preferences directly, cultivar diversity also likely reflects aspects of demand and can help reveal insights into the market preference for certain species. Species that are more widely traded and utilised will have had more efforts made to develop cultivars and vice versa, supporting the notion that market preferences are a key driver of introduction effort with bamboos, as is the case with other economically valuable plant taxa. As far as we know, the link between cultivar development and utility of a species with respect to increasing the probability of introduction and invasions has not been explored for other plant groups.

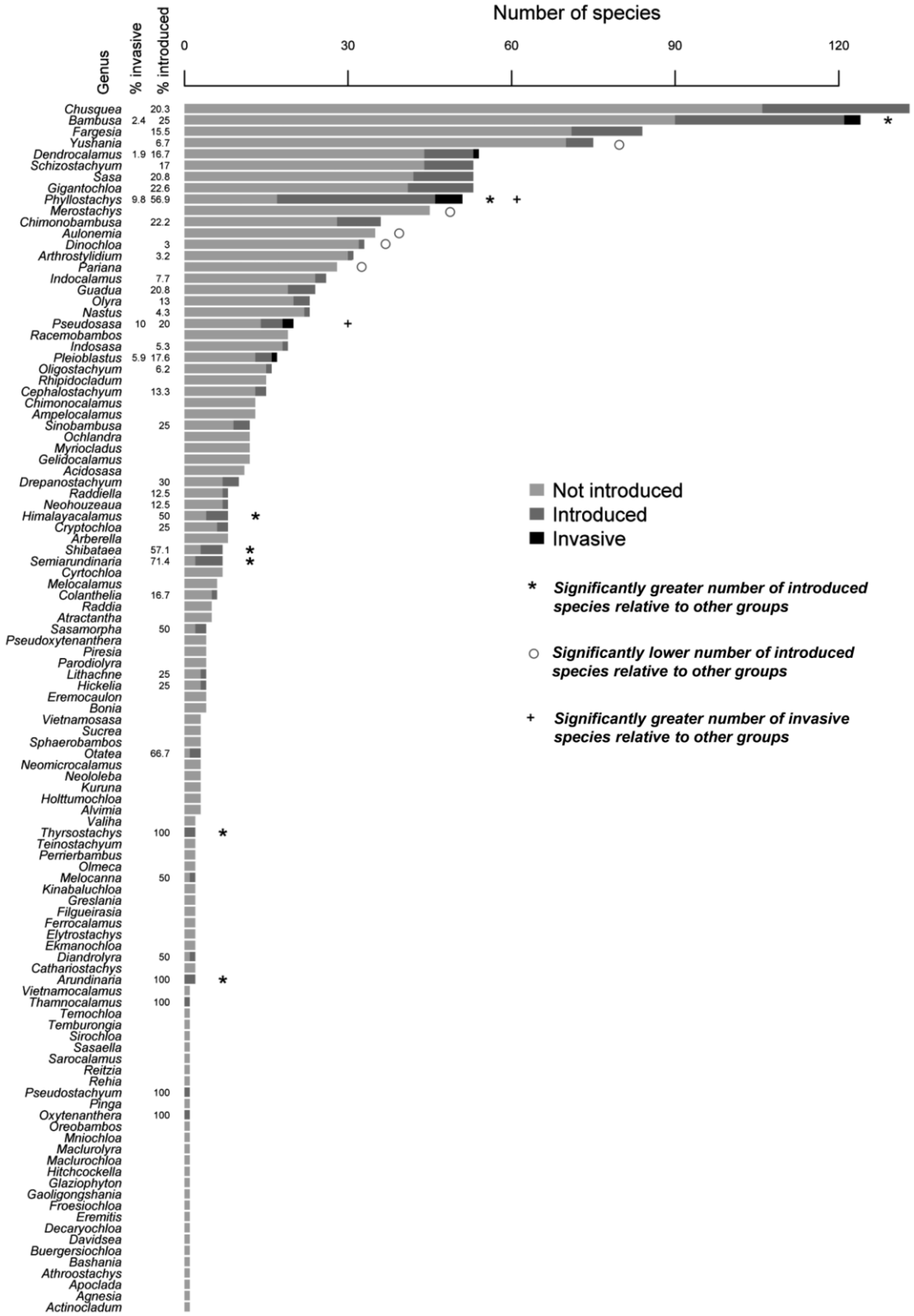

Figure 2.4 Number of bamboo species found within each genera. Shading indicates the status of the species (not introduced/introduced/invasive). Significance was calculated using Fisher's exact tests between numbers of introduced compared with non-introduced species and numbers of invasive compared with non-introduced species across genera.

2.5.3 Selection of traits

Horticulture directly facilitates the movement of species, but it also provokes the selection of certain traits that can increase establishment and the invasion potential of propagules once introduced (Mack 2000, Kowarik 2003, Anderson *et al.* 2006, Martınez-Ghersa and Ghersa 2006, Dehnen-Schmutz and Touza 2008). Linking traits to the success of invasive species has been a strong focus of invasion science and many studies have revealed generalities across many taxonomic groups. Production of large numbers of seeds, fast growth rates and large plant size are some examples of traits positively associated with invasiveness (Cadotte and Lovett-Doust 2001, Pyšek and Richardson 2007, van Kleunen *et al.* 2010).

We found that traits likely related to economic benefits are important in bamboos. Culm attributes were associated with the status of species—whether they had been introduced and were invasive; in particular there was an over-representation of introduced and invasive species with greater dimensions. This may be because the culm is a valuable aspect of the plant, and there has been an incentive to select bigger bamboos to increase production of woody biomass and in general produce larger poles (Kleinhenz and Midmore 2001). However, culm traits did not explain why Asiatic species have been more introduced (and become invasive) than bamboos from other parts of the world. We found that neotropical woody bamboos (of South and Central American origin) were similar to woody bamboo groups in terms of size. Other traits that are important for bamboo as a construction material, which we were unable to test, include culm wall thickness, culm flexibility and internode length.

We expected that the type of clonal growth in bamboos would be an important determinant of invasiveness because bamboos rarely proliferate sexually. It is often suggested in the literature that species that produce long rhizomes (i.e. runner species) are more aggressive than species that produce short rhizomes (RHS 2015). However, we found that both running and clumping species have become invasive. Therefore, the pattern of clonal growth did not clearly separate invasive from non-invasive species and other factors such as human usage, propagule pressure and residency time, need to be considered in any discussion of invasiveness in bamboos.

Species belonging to the genus *Phyllostachys* are most often referenced regarding their ability to spread widely due to fast growth rates and extensive sympodial systems of rhizomes, features which can lead to the formation of monocultures (Isagi and Torii 1997, Suzaki and Nakatsubo 2001). The formation of dense stands can result in a decline in biodiversity through the exclusion of native species (Okutomi *et al.* 1996, Yang *et al.* 2008, Huai *et al.* 2010, ShangBin *et al.* 2013). *Phyllostachys* species have also been shown to invade on a more localised scale,

such as in horticultural garden settings (RHS 2015). In the United States, *Phyllostachys* species (typical examples being *P. aurea, P. aureosulcata*, and *P. edulis*) are distributed and planted as popular ornamental and garden screening plants. However, perhaps due to lack of management and knowledge in maintaining the underground rhizome system, there are reports of populations that have escaped and become naturalized to the extent that they have been shown to occupy 71 588 acres of forests in the US (Miller *et al.* 2008). *Phyllostachys* can also cause a nuisance in urban areas (Connecticut Invasive Plants Council 2011, Joint Standing Committee Hearings 2013). Reported issues in urban areas include structural damage to property from emerging shoots, colonization of gardens and neighbouring land, difficulty and high costs of removing populations due to robust root systems (Joint Standing Committee Hearings 2013). There have been moves to regulate, at the county and state level, the planting and sale of running species (Joint Standing Committee Hearings 2013). With increasing examples of issues surrounding the planting of *Phyllostachys* species, it is likely that other temperate bamboos with similar growth habits and uses will cause similar problems.

2.5.4 Expansion in the native range

Aspects of the native range have been found to influence the invasiveness of species. For example, species originating from regions with high phylogenetic diversity are more likely to be successful invaders, perhaps because they have more competitive traits (Fridley and Sax 2014). All invasive bamboos originated from Asia, but there was no evidence of a significant phylogenetic signal indicating a particular lineage or clade of bamboo that may be a source for invasive species. This suggests that other factors such as human-mediated usage are more important in explaining invasiveness. However, the corollary of the above observation is that areas with low species richness are likely to be highly invasible (Fridley and Sax 2014). In terms of recipient regions, we did find that the majority (8 out of 12) of the areas where bamboo invasions were recorded were islands (areas of low general native plant diversity and specifically low native bamboo diversity).

Another important factor associated with phylogenetic diversity and invasiveness was the size of the range of species. Species with larger native ranges tend to have greater invasion success, because they possess traits that have facilitated establishment over a wide range of environmental conditions e.g. (Pyšek *et al.* 2009a, Pyšek *et al.* 2009b, Moodley *et al.* 2013, Novoa *et al.* 2015). Range size has also been manipulated by human-usage, as many species have been moved and cultivated beyond the extent of their native provenance. We were unable to account for native range size as delimiting ranges for bamboos was difficult, especially in

Asia where there has been extensive exchange and cultivation of species over millennia (Yuming *et al.* 2004, Lobovikov 2005). We found many records for the movement of Asiatic species to other continents, but much less information on within-continent movements. For example, Moso bamboo (*Phyllostachys edulis* syn. *P. pubescens*), one species of about 583 native to China, has become widespread (both through natural spread and cultivation) and is estimated to make up 80 % of bamboo cover (5 million ha) across the country (Bowyer *et al.* 2014). Its distribution is still increasing, in part due to extensive plantings but also due to disturbances in mixed forests (Gagnon and Platt 2008) that have facilitated its increased abundance and dominance in some vegetation types (Yang *et al.* 2008, Huai *et al.* 2010, ShangBin *et al.* 2013, Song *et al.* 2015, Tokuoka *et al.* 2015, Xu *et al.* 2015, Rother *et al.* 2016).

In general, expansion and weedy behaviour of plants in their native range has been shown to be a good indicator of invasive potential (e.g. Richardson and Bond 1991). As past introductions of bamboos have favoured a certain set of species from particular regions, there is significant potential for bamboos in other parts of the world such as South America to be utilised in the future. Such species that have been identified as being highly competitive and weedy in native regions have the potential to become invasive in new areas given the opportunity, and should be carefully evaluated for future introductions. Some examples of bamboos that are found to be weedy and have had impacts in their native ranges are *Pleioblastus arenteostriatus* (syn. *P. chino*; Kobayashi *et al.* (1998); Tokuoka *et al.* (2015)), *Fargesia nitida* (Wang *et al.* 2012) and *Sasa chartacea* (Tomimatsu *et al.* 2011) in East Asia. *Ochlandra travancorica* (Dutta and Reddy 2016) and *Melocanna baccifera* (Majumdar *et al.* 2015) from India, and *Guadua tagoara* (Rother *et al.* 2016) and *Guadua paraguayana* (Galvão *et al.* 2012) from South America have not been widely moved outside of their native ranges but, given the observed weedy tendencies of these species in their native ranges, they could pose risks if future introductions were to occur.

Without accurate records on the original ranges of many taxa, it is difficult to comment on the rate of spread and the extent of invasions. We suspect that invasions of some species may have gone unnoticed. This is due to scant information on the native provenance in some regions, and problems with identifying some bamboo species. This is the case where some species are widely dispersed at the continental level and are assumed to be native while they may well be introduced in parts of their current range.

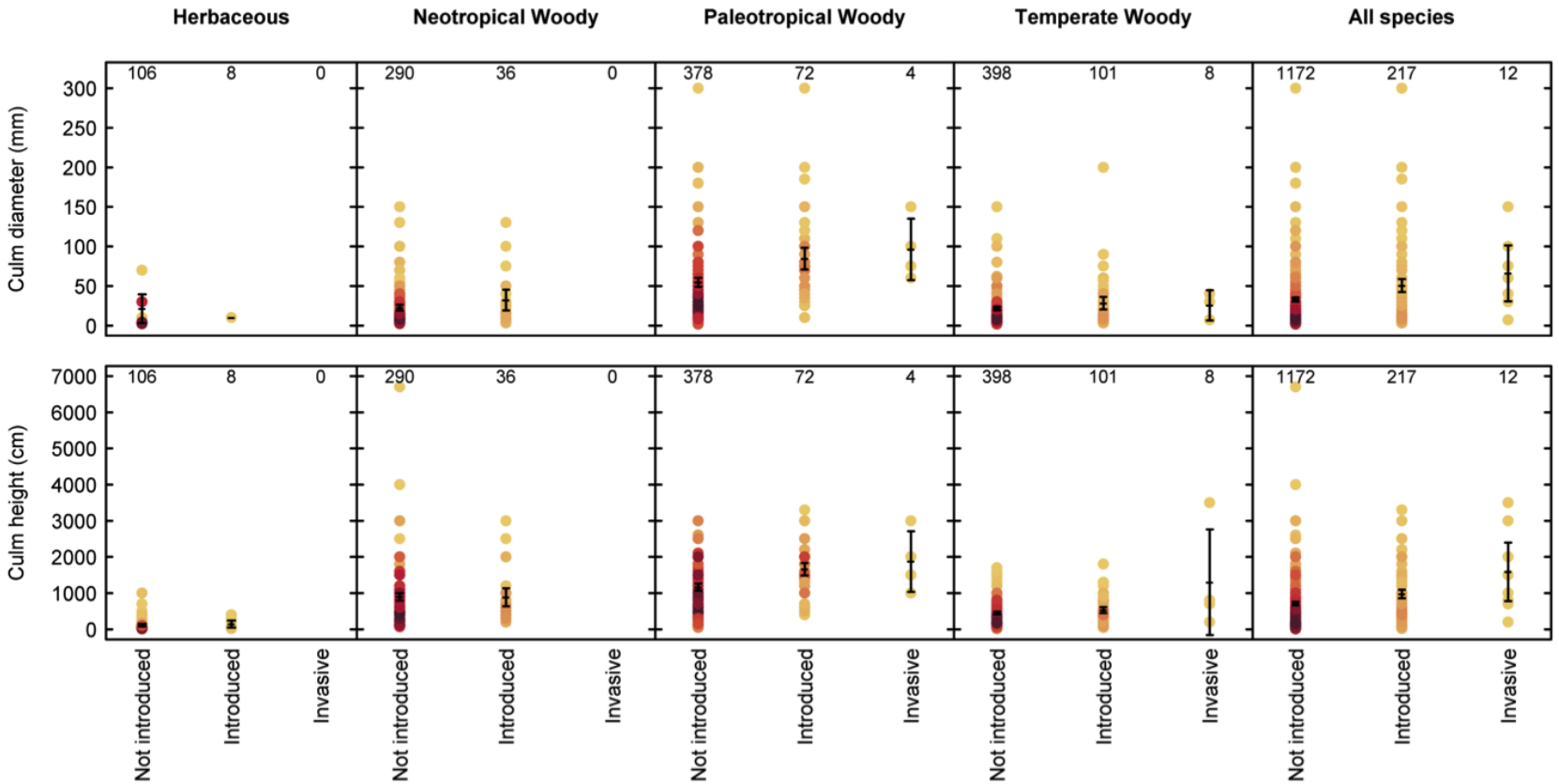

Figure 2.5 Culm diameter (mm) and culm height (cm) of bamboo species (error bars indicate 95 % confidence intervals) across lineages, and grouped by status. Shading indicates the number of species at each point, with lighter yellow representing less species and darker red shades representing many species. Numbers at the top of each plot indicate the number of species (in which data were available) for the corresponding status group.

2.5.5 Extent of invasions

Overall, we found few invasive species of bamboos (0.7 % of taxa) despite the diversity, high rate of dissemination and utilization of various species globally; we had expected this number to be higher. The low number of invasive bamboos is in marked contrast with other taxa within the grass family, which have been noted for containing a high concentration of invasive species (studies estimate between 6 and 10 %; Pyšek (1998) ; Visser *et al.* (2016)). Bamboos seem to be an exception in the group. Some of the most extensive invaders in the grass family are large-statured woody grasses, notably *Arundo donax* and *Phragmites australis* (Lambert *et al.* 2010, D'Antonio *et al.* 2011). These invasive woody grasses mostly rely on asexual means for spreading via the rhizome systems like many bamboos (Nadgauda *et al.* 1990). There is scope to investigate such mechanisms in explaining the ability of some large-statured woody grass species to be widespread invaders and why this appears not to be the general case with bamboos.

When compared with other plant taxa outside of the grass family, bamboos have a similarly low occurrence of invasive species; in the group of trees and shrubs it was found that between 0.5 % and 0.7 % of the global pool of species had become invasive (Richardson and Rejmánek 2011), and for the families of Proteaceae (Moodley *et al.* 2013), Araceae (Moodley *et al.* 2016) and Cactaceae (Novoa *et al.* 2015), 2 %, 0.5 % and 3 % are invasive, respectively.

We discounted invasions in 26 regions (including those involving three additional species) as references could not be verified or were inaccessible. We suspect that the listing of some bamboos as invasive may be unwarranted (or inflated). This is the case with *Dendrocalamus strictus*, for which it was difficult to disentangle the rate of spread versus impacts, as there was not an explicit distinction in many references [Supplementary Material]. In many cases, a long history of planting of bamboos gave the appearance of a prolific, spreading population, whereas the expansion of the population has in fact been minimal or non-existent (O'Connor *et al.* 2000). For this reason, it is important that standardized and measurable criteria be adopted for defining what ‘invasive’ means for bamboos.

2.6 CONCLUSION

Our results suggest that invasiveness in bamboo species is currently more a function of which species have been moved by humans and for what purposes than of inherent differences

between species. Certain taxa, for historical and geographical reasons, have rarely been introduced. In particular, native South American bamboos have not yet been widely disseminated. Such taxa might hold promise for future utilisation, and could become invasive. By contrast, past introductions (especially from Asia) have radically rearranged the global distribution of some bamboo species, and new trends in the drivers of introductions are rapidly changing the dimensions in this natural experiment in biogeography. The emergence of large-scale bamboo plantations in new regions of the world represents a fascinating new stage in the bamboo story. There is an urgent need for science-based guidelines to minimize invasion risks.

3 Does origin determine environmental impacts? Not for bamboos

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Author contributions: S.C., J.R.U.W., J.J.L.R and D.M.R. conceived the idea. S.C. compiled and scored the data with help and advice from S.K. S.C. led the writing of the manuscript with inputs from all co-authors.

3.1 ABSTRACT

Negative environmental impacts can result from the human-mediated breakdown of biogeographic boundaries that historically shaped species distributions leading to rapid population expansions, i.e. from biological invasions. However, the alteration of natural ecosystems by humans has created opportunities for both native and non-native species to become weedy. We assessed whether origin status (native or non-native) matters for the type and magnitude of environmental impacts caused by bamboos (Poaceae: Bambusoideae). We used a systematic global literature search and the International Union for Conservation of Nature's (IUCN) Environmental Impact Classification of Alien Taxa (EICAT) scheme as the basis for scoring impacts of bamboo species. We found that the type and severity of recorded impacts were similar in the native and non-native ranges of weedy bamboos, and that the habitats in which impacts are most often reported (i.e. temperate and tropical forests) were also the same. Origin was not a strong predictor of environmental impacts for bamboos. Rather, impacts are likely to be a response to human-mediated land transformation and disturbance of forests. Further research on the mechanisms whereby bamboos impact other species is needed to guide management strategies in their native ranges and as input to risk assessments for new introductions and plantings.

3.2 INTRODUCTION

Many non-native species profoundly alter communities they invade through competition, hybridisation, disease transmission and other mechanisms (Kumschick *et al.* 2011). Such

impacts threaten the presence of native taxa, and have contributed to species extinctions (Bellard *et al.* 2016). The extent and magnitude of impacts of invasions are increasing globally, and methods for identifying and quantifying them more efficiently are urgently needed. The link between impact and biogeographical origin is, however, contentious. Non-native species are sometimes the drivers and other times the result of global change (MacDougall and Turkington 2005), and many plant species are agricultural and/or environmental weeds, even within their native ranges (Randall 2017).

Some authors have suggested that further comparisons are needed for species that are weedy both in their native and non-native ranges to make progress in the field of invasion science (Hufbauer and Torchin 2008). For example, identifying weedy native plants can be useful for management; species that are prone to becoming weedy (i.e. expanding rapidly, encroaching or having transformative impacts) following disturbance, are also more likely to become problematic when introduced to similar habitats (Caley and Kuhnert 2006, Davis *et al.* 2010). Secondly, controlling weedy natives and non-natives concurrently is often necessary to promote the rehabilitation of ecosystems. When weedy natives become dominant they often reduce populations of other native species (Yelenik *et al.* 2004). And, when management focuses on non-natives only, e.g. through clearing, resultant disturbances often cause native communities to become dominated by other weedy or ruderal species.

Though native species can display weedy habits under specific conditions, there is general consensus that invasive non-native species have greater environmental impacts (Meiners *et al.* 2001, Simberloff *et al.* 2012, Paolucci *et al.* 2013, Hassan and Ricciardi 2014, Taylor *et al.* 2016). A 40-year study reviewing abandoned agricultural land found that invasions by non-native species had a stronger effect than native weeds on overall species richness (Meiners *et al.* 2001). This pattern is generally consistent for plants (Simberloff *et al.* 2012, Taylor *et al.* 2016) and animals (Paolucci *et al.* 2013, Hassan and Ricciardi 2014). These findings suggest that origin status (e.g. native or non-native) influences the level (e.g. magnitude) and type (e.g. mechanism) of environmental impacts that occur when a species becomes weedy and forms a dominant component of communities.

Bamboos (Poaceae: Bambusideae; c. 1600 species) are an excellent group for exploring the relevance of biogeographic origin when considering impacts caused by weedy species. A growing number of studies have addressed the impacts of bamboos in both their native and non-native ranges for several reasons: (1) Bamboos have an extensive distribution both naturally and

because they have been widely redistributed around the world by humans (Canavan *et al.* 2017b); (2) bamboos are often dominant components of vegetation; a change in abundance can therefore have large effects on community structure and functioning; (3) species that are known to have impacts are not always the same as those with capacity for rapid dispersal i.e. to become invasive (Richardson *et al.* 2011, Canavan *et al.* 2017b); and (4) bamboos are perennial forest grasses and therefore have a unique interaction with trees compared to other grass groups (Soderstrom and Calderon 1979). Forest systems are generally less studied in invasion science than other major habitat types, such as grasslands (Levine *et al.* 2004), and they are considered to be generally inherently less susceptible to invasions by non-native species than most other habitats (Crawly 1987, Von Holle *et al.* 2003). Therefore, studying bamboos might provide insights into a facet of invasion science that has not received much attention (Martin *et al.* 2009).

We reviewed the literature on the environmental impacts caused by invasion (i.e. the spread of non-native species) and expansion (i.e. the spread of weedy native species) of bamboos. We then used the International Union for Conservation of Nature's (IUCN) Environmental Impact Classification of Alien Taxa (EICAT) scheme (Blackburn *et al.* 2014, Hawkins *et al.* 2015) to score the impact type and magnitude in the native and non-native ranges. We expected to find greater impacts in the non-native range where bamboos might have fewer pressures controlling their populations, and that the types of impacts would be different for native and non-native species. We also tested whether the habitats where impacts are described are similar in native and non-native ranges.

3.3 METHODS

3.3.1 Species Selection

Because bamboos are a large taxonomic group (1600 spp.) we selected a subset of species for our literature search. Taxa were selected based on two criteria: (1) In line with previous impact assessment reviews (Kumschick *et al.* 2015a), we chose species that have been introduced to multiple regions (≥ 5 countries according to (Canavan *et al.* 2017b); (2) As we were also interested in impacts within the native range, we used the Global Compendium of Weeds (GCW) database to identify all bamboo species for which terms associated with weediness (e.g. garden thug, native weed, etc.) have been applied in the literature (Randall 2017). Both criteria were needed to target literature of impacts in the native and introduced range. An additional general search was carried out using the term “bamboo” and key terms.

To assess whether our method was suitable for capturing most of the literature on impacts of bamboos, we tested whether our selection criteria for taxa (by number of regions) was related to the amount of literature available (**Figure S3.1**). We searched for "Species name" in a general online search platform (Google) and academic search platforms (Google Scholar + Web of science), and we recorded the number of search results returned for all bamboo species. All searches were done in English. However, we included articles in other languages given they had an abstract in English (although this led to a lower confidence score in the impact frmaework, see section 3.3.2 below). We used a non-parametric (Kendall's tau) correlation to test whether the number of search results returned per species on each online platform (Google, Google scholar and Web of Science) was related to the number of regions of introduction (country level). All analyses were performed in R v3.2.1 (R Core Team 2015).

3.3.2 Impact framework

The Environmental Impact Classification for Alien Taxa (EICAT) scheme, which has been adopted by the IUCN, offers a standardised tool for producing impact assessments. To date, studies using EICAT have been published on birds (Evans *et al.* 2016), amphibians (Kumschick *et al.* 2017a, Kumschick *et al.* 2017b) and some mammals (Kumschick *et al.* 2015b, Hagen and Kumschick 2018), but not yet for plants. In assessing the impacts of bamboos, we followed the guidelines of Hawkins et al. (2015) including: (1) intensive literature search of selected taxa of interest; (2) filtering of relevant literature pertaining to impacts; (3) scoring of the type and magnitude of impacts from the literature; and (4) evaluation of the data quality of the literature scored.

We performed a systematic search of the peer-reviewed literature of our selected taxa using binomial species names on Google Scholar. Species were searched independently, and with additional key terms ("impacts" OR "invasive"). Results were filtered by relevant titles and abstracts of papers. For literature on bamboos in their native range, we only included references of impacts when the expansion or presence of the species was due to disturbance caused by human activities which has changed the "natural" and historical abundance and distribution in that region (e.g. logging of forests, agriculture fragmentation of the habitat, changes associated with climate change etc.). For all literature we noted the habitat type where impacts were recorded, where applicable. This was not an exhaustive search, but is likely to have captured data for the vast majority of bamboo species for which impacts have been recorded.

3.3.3 Scoring impacts and analyses

Impacts reported in the literature were evaluated and scored according to Hawkins et al. (2015). For magnitude of impact or impact level, species were scored (Minimal Concern, Minor, Moderate, Major, Massive) across 12 categories. The literature was also evaluated to determine the quality of evidence (low, medium, and high; e.g. high confidence that there is direct observational evidence to support the scoring and classification of a given impact; see **Figure S3.2**). Publications in which the origin status (native or non-native) was unknown were excluded. To test whether the distribution of references across different impact levels was the same between the native and non-native ranges we used a Wilcoxon signed-rank test. To test whether the number of references by origin status was different across mechanism types, and also for habitat types, we used a two- way Chi squared test.

Table 3.1 Selected examples of the three most common environmental impacts recorded for bamboos.

Impact mechanisms	Region (Status)	Examples
Competition	Argentina (native)	*Chusquea ramosissima* Lindm quickly moves into open gaps following timber extraction to dominate the forest understory. Considered to be one of the most aggressive colonisers in the region, as it suppresses the growth of emerging trees and saplings by filling available space and shading out light (Montti *et al.* 2009).
	S. America (native)	The expansion of other native bamboos (including *Guadua tagoara* (Nees) Kunth) is also considered a major threat to the South American Atlantic Forest (Araujo 2008; Lima et al. 2012). The dieback of trees from competition with bamboo is the most commonly reported impact. This leads to the simplification of plant composition, as the aboveground biomass of bamboo increases on the invasion front so does tree mortality rate (Teixeira & Oatham 2001; Saroinsong et al. 2006; Huai et al. 2010).
	China (native)	The expansion of *Phyllostachys edulis* in native forests in China is associated with: changes to the spatial distribution of plant communities (Huang *et al.* 2009); declines in the diversity of birds (Yang et al. 2008); declines in forest floor myrmecofauna (Touyama et al. 1998); increased microbial biomass and diversity in areas where moso bamboo dominates compared to native broadleaf forests (Xu et al. 2015).
Other: indirect effects	Argentina (native)	The expansion of dwarf bamboo (*Sasa* sp.*)* affects acorn seed dispersal by wood mice; fewer acorns are found in areas where *Sasa* dominated compared to where it had been removed (Iida 2004).
	Argentina (native)	Bamboo abundance has indirect effects on animal communities by changing the behaviour of animals: the continued expansion of bamboo is thought to affect the dispersal patterns of big seeds by mammals where big mammals had a preference for areas not dominated by native bamboo (Gallardo *et al.* 2008).
	Seychelles (alien)	Naturalised *Bambusa vulgaris* was associated with changes to the density and foraging behaviour of the vulnerable giant millipede; areas not dominated by bamboo were preferred for foraging (Lawrence *et al.* 2013)

Chemical	China (native)	*Phyllostachys edulis* expansion is associated with changes to nutrient/ pollutant fluxes in forest floors including: changes to C and N properties of the soil, although inconsistent patterns have been found depending on habitat type (Lin et al. 2014); changes to soil community structure (Chang and Chiu 2015; Umemura and Takenaka 2015); less soil nitrogen available and slower cycling rates of nitrogen compared to secondary evergreen broadleaved forest, which is potentially contributing to soil degradation (Song et al. 2017); higher silica content in bamboo litterfall was observed compared to other forest types in Japan, as well as higher silica concentrations in surface soils (Ikegami et al. 2014). This results in huge amounts of biogenic pools of Silica accumulate on forest floors colonised by bamboo (Umemura & Takenaka 2014).
	Japan (alien)	Moso bamboo invasions are associated with increased soil pH into Hinoki forests

3.4 RESULTS

3.4.1 Species selection

138 bamboo taxa were systematically searched for impacts. The search represents all taxa that are likely to have recorded impacts in the literature (See **Figure S3.1**). The remaining bamboos that were not evaluated in this study are therefore classed as NE—Not Evaluated under the EICAT scheme (although some of these can be considered as NA – No Alien Population according to Canavan et al. 2017). Of the 138 taxa that were included in the study, we found 65 references which contained details on 20 species for which recorded environmental impacts could be scored using the EICAT scheme. The 115 species for which we could not find literature for were classified as Data Deficient.

The number of references reporting impacts has increased over time, although this could be related to a general increase in online literature (**Figure 3.1d**) and/or research interest in the group. Regarding the availability of literature for bamboo species, we find that the number of regions to which a species has been introduced is positively correlated with the number of online search results returned per species on Google (*tau*=0.405, p-value < 0.001), Google Scholar (*tau*=0.384, p-value < 0.001) and Web of Science (*tau*=0.385, p-value < 0.001; See **Figure S3.1**). This suggests that we have identified the majority of bamboo species for which impacts have been formally recorded, which is ~1% of all species.

3.4.2 Scoring impacts using EICAT

3.4.2.1 Species and regions

There was an equal representation of impacts reported in the native and non-native range of bamboos (n=32 references) for both groups, and an additional three papers where the origin was unknown (Table S1). More species (n=13) were associated with impacts in the native range than in the introduced range (n=9). Almost half (28/60) of all impact references were for the species *Phyllostachys edulis*, for which there was near equally representation in the native and non-native ranges of the species (**Table S3.1**). The only other species for which impacts were recorded in both the native and non-native ranges was *Bambusa tulda*.

3.4.2.2 Mechanism of impact

Impacts of bamboo were associated with four mechanisms as defined by Hawkins et al. (2015): competition, poisoning/ toxicity, structural, and chemical changes to an ecosystem (Figure 1a). The number of references for impacts across each mechanism was not significantly different between non-native and native ranges, X^2 (4, N = 62) = 4.450, p=0.35. The mechanism that most frequently led to impacts was competition, followed by chemical changes to an ecosystem (Figure 1a). We also found no significant difference (W = 5, p=1) in the distribution of references across impact levels between native and non-native ranges (**Figure 3.1b**).

3.4.2.3 Habitat and distribution

Impacts were predominantly reported in tropical and temperate forests in both non-native and native ranges, and also in plantations (**Figure 3.1c**). There was no significant difference in the number of references for habitat type by origin status, X^2 (3, N = 65) = 5.778, p=0.12. We also found that impacts in the native range are mostly reported from regions with large native bamboo floras, specifically in Asia and South America (**Figure 3.2**). Impacts of non-native bamboos were also recorded in these regions, and in Central America, North America, and Africa.

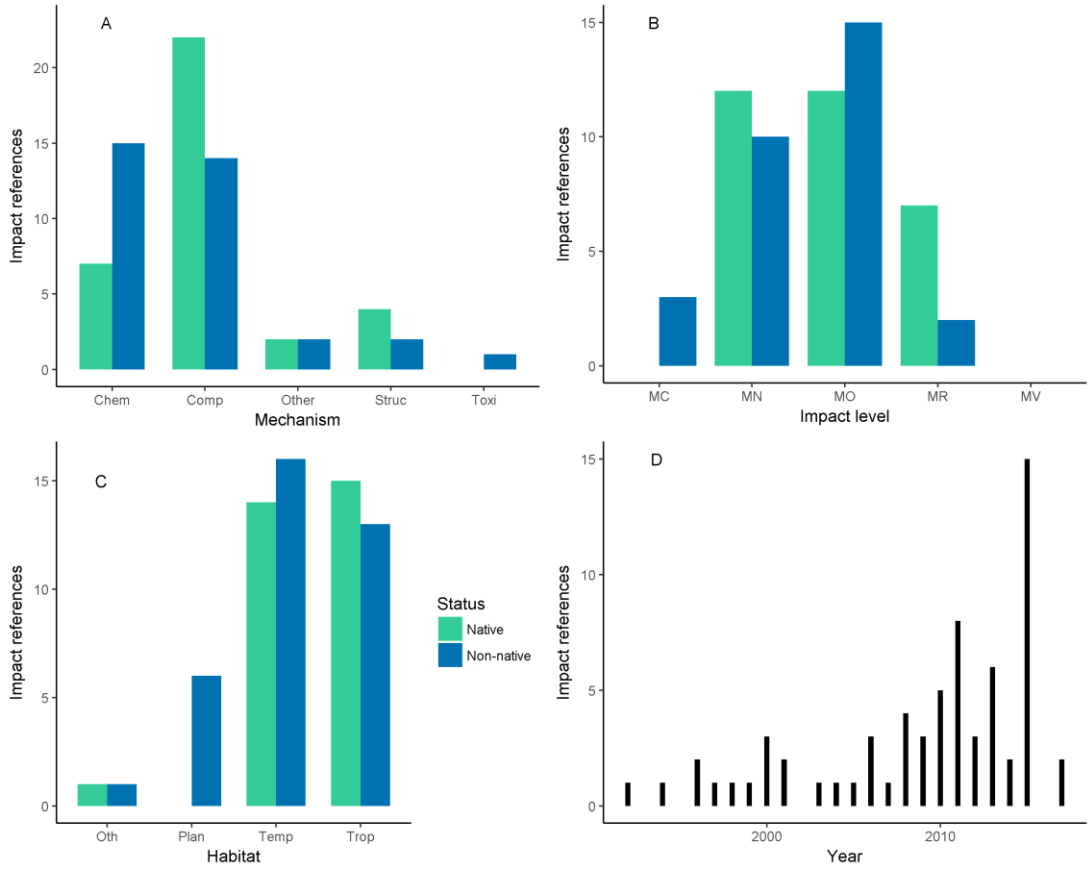

Figure 3.1 A comparison between impacts in the native and non-native range of bamboos using a systematic global literature search and a modified version of the International Union for Conservation of Nature's (IUCN)'s Environmental Impact Classification of Alien Taxa (EICAT) scheme. Colours indicate the number of impact references reported in the non-native (light green) and native (dark blue) ranges for: (A) type of impact or mechanism (chemical, competition, other, structural, and toxic/ poisoning); (B) impact level (MC- minimal concern, MN-minor, MO-moderate, MR-major and MV-massive); and (C) habitat where the impact is occurring (other, plantation, temperate forest and tropical forest). (D) the number of impact references found online by year of publication that address environmental impacts of bamboo.

3.5 DISCUSSION

Contrary to our expectation, we found that biogeographic origin was not a clear indicator of the type and magnitude of environmental impacts caused by bamboos

(**Table** 3.1). The high incidence of reported impacts in the native ranges of bamboos relative to the non-native range is perhaps unusual compared to what has been observed for other taxonomic groups (Kumschick *et al.* 2011). This may be partially explained by the historically high usage of bamboos by humans within their native ranges, which has undoubtedly altered their natural abundance and distribution, especially in Asia. In many cases, the exact native provenance of a species is disputed or unknown (e.g. *Bambusa vulgaris*).

An example of a species with impacts in its native range is *P. edulis* (moso bamboo), a large temperate species that is the most commonly cultivated bamboo for timber in China. Although native, this species has become increasingly problematic over the past few decades (Wang and Stapleton 2008). This is in part because of the increased demand for bamboo products which has led to mixed-species forests (bamboo and trees) being converted to bamboo monocultures. Other indirect types of human influence such as climate change have also been reported to cause changes in bamboo abundance, facilitating impacts in their native range, e.g. the spread of *P. edulis* forests to higher altitudes in the Tianmu Mountains in China (Song *et al.* 2013), and the expansion native dwarf bamboo (*Sasa kurilensis)* into relatively undisturbed alpine snow-meadows in Japan (Kudo *et al.* 2011, Kudo *et al.* 2017).

In South America, several reports exist of native bamboos being problematic in Amazonian forests (**Table** 3.1). There is evidence that pre-Columbian civilisations altered these forests to favour species that were of value to humans (Levis *et al.* 2017). Watling et al. (2017) investigated the impacts of humans over millennia and found that these cultures most likely took advantage of bamboo life cycles (e.g. entire senescence of populations following seeding) to deforest areas for agriculture. This could have had legacy effects on the contemporary distribution patterns of native bamboos in these regions.

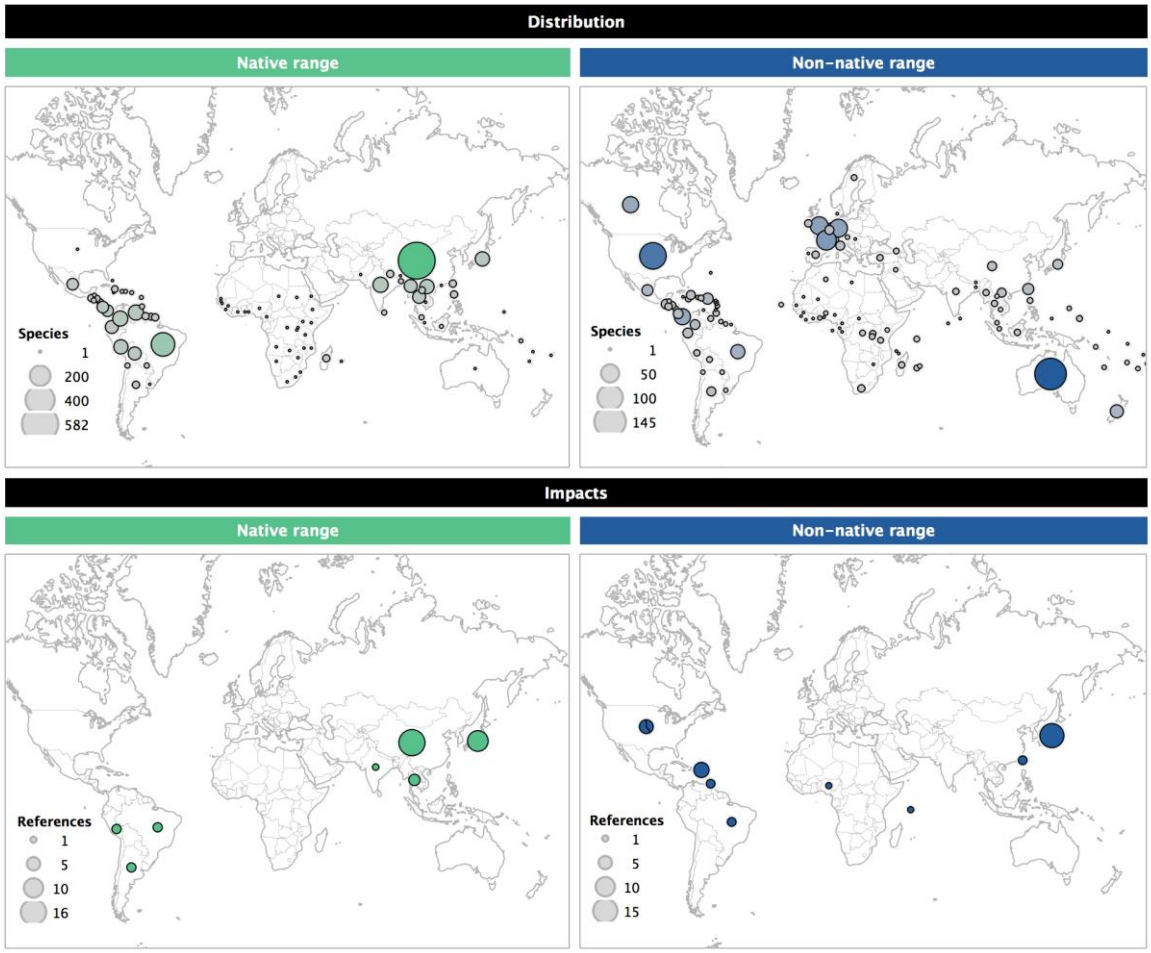

Figure 3.2 The geographic distribution and localities of reported impacts of native and non-native bamboos. Top: the native and non-native distribution of bamboos (data retrieved from Canavan et al. 2017). The non-native distribution includes species that have been introduced to a region but may not have escape cultivation. Bottom: Localities where impacts have been reported in the native and non-native ranges of bamboos based on a systematic global literature search using a modified version of the IUCN's Environmental Impact Classification of Alien Taxa (EICAT) scheme. Circle size is proportional to the diversity of bamboos in a given country/ region (top) and to the number of references (bottom). Note that species and references in Hawaii are grouped with the continental United States.

Almost all examples of bamboos having impacts are in temperate and tropical forests, which we expected in the native range where bamboos occur naturally. However, this was also true for impacts in non-native ranges, which was unexpected for two reasons: (1) Forests are generally considered to be less susceptible to plant invasions (although some authors have attributed this to study biases towards grasslands and scrublands (Martin *et al.* 2009)); (2) Bamboos have been extensively introduced and cultivated outside of forest systems, including highly transformed ecosystems (e.g. urban areas, agricultural land) and disturbed habitats that tend to be more vulnerable to plant invasions, yet, impact studies have still mainly observed forest invasions (D'Antonio and Meyerson 2002). This might indicate that habitats of lesser ecological value

(e.g. roadside verges, abandoned agricultural land, etc.) have not been studied in as much detail to determine invasion impacts, or that bamboos just have greater potential for impacts in forests.

There are several possible reasons for this pattern. The bamboos found to have impacts have clear physiological adaptions that make them highly competitive in heterogeneous light environments, e.g. the understory of forests. Also, bamboos are often dominant components of the vegetation where they occur which means that a change in their abundance can have a big effect on community structure and functioning. The dense underground clonal root systems can further facilitate competitive expansion by storing and supplying energy for growth when needed, even when little light is available (Wang *et al.* 2016). For example, bamboos overwhelm tree seedlings following canopy disturbances by quickly colonising space and capturing available light (Larpkern *et al.* 2011). Bamboos can also produce large amounts of biomass in short periods of time, which can sustain dominance by supressing the growth of neighbouring vegetation through the build-up of leaf litter. The lack of top-down regulation of bamboos, through herbivory, may also enhance their competitive ability.

When bamboos replace trees their distinct morphological and physiological traits often lead to changes in biogeochemical processes, i.e. chemical changes to ecosystems (Wu *et al.* 2008, Chiwa *et al.* 2010, Song *et al.* 2016). For example, the build-up of leaf litter leads to the accumulation of silica pools in the soil (Ikegami *et al.* 2014), slower rates of decomposition (O'Connor *et al.* 2000), and altered nutrient cycling (Song *et al.* 2015, Song *et al.* 2016). The high density of roots and rhizomes can also lead to changes in hydrological processes (Shinohara and Otsuki 2015), e.g. increased surface runoff of rainfall (Ide *et al.* 2010). These impacts can alter biotic communities, e.g. changing the abundance and diversity of bacterial (Lin *et al.* 2014), ant (Touyama *et al.* 1998), and microbial (Chang and Chiu 2015) communities in the soil, as well as animal behaviour (Iida 2004, Lawrence *et al.* 2013).

The physical removal of bamboo biomass can reverse some impacts, especially by increasing tree recruitment rates (Larpkern *et al.* 2011). For example, the removal of dominant *P. edulis* over a seven-year period was associated with the passive restoration of plant species diversity (Bai *et al.* 2013). Moderate thinning of stands and clearing of dead biomass of native bamboos along riverbanks in Japan leads to increased biodiversity in riparian areas (Suzaki and Nakatsubo 2001). Similarly, the removal of native dwarf bamboo species has led to the recovery of native species and increased diversity in alpine communities (Kudo *et al.* 2017). This shows that managing weeds and reducing their dominance, where applicable, can be an effective

conservation tool in areas affected by bamboos (regardless of their status as native or non-native species). A better understanding of not just a species' native range but also its natural abundance within its range is needed when managing impacts.

Although this review covered most of the available studies of impacts caused by bamboos (Cf. **Figure S3.1**), the sample size was small and likely subject to sampling bias (only 20 of the 138 bamboo taxa searched could be evaluated using the EICAT scheme). There was literature that we were unable to access, for example, articles published in local Chinese journals. More impact studies covering a greater diversity of bamboo species is needed to determine whether the findings of this study hold true for bamboos in general. The results nonetheless indicate that bamboos have the potential to cause major impacts in forest systems. We also note that there was a prevalence of impact studies involving *Phyllostachys* species, especially *P. edulis*. Species in this genus are 'runners', that is, they send underground rhizomes to produce shoots several meters from parent plants. This growth form enables them to spread more rapidly than other species, such as those with a clumping growth form (Lieurance *et al.* 2018b). The overrepresentation of this genus in studies reporting impacts in bamboos suggests that impacts are common and dramatic, and that further impacts are very likely in new areas where *Phyllostachys* species are introduced and planted.

Although our assessment was restricted to environmental impacts, weedy bamboos also have diverse socio-economic impacts in both their native and non-native ranges (Smith *et al.* 2015b). Most notable is the association between mass-seeding events of bamboos and famine (Nag 1999, Singleton *et al.* 2010). Prolific seeding leads to booms in populations of rodents and other small mammals which feed on the bamboo seeds (Numata 1970). Once the seeds are depleted the rodents move to neighbouring agricultural land where they destroy food stocks (Nag 1999, Singleton *et al.* 2010). While not yet recorded from the introduced range as far as we know, such impacts have been identified as risks associated with widespread cultivation or invasions of bamboos (Smith *et al.* 2015b).

3.6 CONCLUSION

We conclude that certain bamboo species are inherently weedy in that they can exploit human-mediated disturbances (e.g. timber extraction and logging in the case of bamboos) to increase in abundance and cause impacts, regardless of their biogeographic origin. To manage such impacts, we need to identify these species. The management of weedy native bamboos has been considered necessary to promote the regeneration of other species, particularly trees, and to

prevent the formation of bamboo monocultures. If these same species were introduced to areas outside their native ranges, we would expect similar impacts to occur and that similar management would be needed. We predict that the species of bamboo that have impacts in the native range will be a threat if introduced to non-native ranges, especially forests. Finally, we hypothesise that the lack of a biogeographical signal for impact (as is evident for many other taxonomic groups), is due to the inherent competitive ability of bamboos, their response to disturbance, and a possible general lack of top-down regulation through herbivory. Further work to understanding these mechanisms and how they vary across other groups is needed to inform objective strategies to ensure the sustainable utilisation of bamboos. Finally, based on the findings here, we suggest that plant species that respond vigorously to disturbance and that do not have strong top-down population regulation might be expected to show less of a biogeographic signal for impact than other species.

4 Tall-statured grasses: a useful functional group for invasion science

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Contribution of authors: SC, DMR and JRUW conceived the idea**.** MV and RJS provided taxonomy expertise and finalising the species list. VL and GB provided risk assessment data. PP, JC, HK, FE, JP, MvK, PW, MW, NM, WD supplied the GloNAF data and some analyses. LAM, GWG, KC, CL, HS, VV, DD and all other authors contributed to discussions, guidance and formation of the functional group with their individual experience working with tall-statured grasses, during a workshop. I started the discussion of the group and led the formation and writing of the manuscript, with the help of all authors.

4.1 ABSTRACT

Species in the grass family (Poaceae) have caused some of the most damaging invasions in natural ecosystems, but plants in this family are also among the most widely used by humans. Therefore, it is important to be able to predict their likelihood of naturalisation and impact. We explore whether plant height is of particular importance in determining naturalisation success and impact in Poaceae by comparing naturalisation of tall-statured grasses (TSGs; defined as grass species that maintain a self-supporting height of 2 m or greater) to non-TSGs using the Global Naturalised Alien Flora (GloNAF) database. We review the competitive traits of TSGs and collate risk assessments conducted on TSGs. Of the c. 11,000 grass species globally, 929 qualify (c. 8.6%) as TSGs; 80.6% of TSGs are woody bamboos, and the remaining species are scattered among 21 tribes in seven subfamilies. When all grass species were analysed, TSGs and non-TSGs did not differ significantly in the probability of naturalisation. However, when we analysed woody bamboos separately from the other grasses, the percentage of TSGs that have naturalised was 2–4 times greater than that of non-TSGs for both bamboos and non-bamboo groups. Our analyses suggest that woody bamboos should be analysed separately from other TSGs when considering naturalisation; within the ≥ 2 m height class they do not naturalise at the same rate as other TSGs. Rapid growth rate and the capacity to accumulate biomass (a

function of height) give many TSGs a competitive advantage and allow them to form monospecific stands, accumulate dense and deep litter mats, reduce light availability at ground level, and alter fire and nutrient-cycling regimes, thereby driving rapid ecosystem transformation. While the height distribution in grasses is continuous (i.e. no obvious break is evident in heights), the 2 m designation for TSGs defines an important functional group in grasses that can improve predictive modelling for management and biosecurity.

4.2 INTRODUCTION

A useful approach in studying alien plant invasions has been to identify broad patterns and correlates of invasiveness and impacts, such as functional groups, and to use these to provide generalisations for management (Vilà and Pujadas 2001, Colautti *et al.* 2006, Pyšek and Richardson 2008, Novoa *et al.* 2015). Functional groups are sets of organisms that share attributes that confer similar morphological, physical, behavioural, biochemical or environmental responses to ecosystem processes (Lavorel *et al.* 1997, Pérez-Harguindeguy *et al.* 2016, Garnier *et al.* 2017). Functional groups can be used to identify species that respond similarly to environmental pressures and are therefore useful for predicting and managing impacts of alien species (Díaz and Cabido 1997, Lavorel *et al.* 1997).

Plant height is considered a key trait for ecological strategies (Grime *et al.* 1988, Westoby *et al.* 2002, Garnier and Navas 2012), and according to Tilman (1982) resource competition theory, resource exploitation is proportional to individual biomass, with larger individuals exploiting a disproportionate amount of resources (DeMalach *et al.* 2016). Many studies have recognised the benefits of increased height for initial colonisation by alien plants, as it is associated with better light capture and competitive ability (Pyšek *et al.* 2012, Moodley *et al.* 2013, Gallagher *et al.* 2015). Among plants, invasions by tall-statured grasses (hereafter TSGs; **Figure** 4.1) are particularly noted for their ability to dominate plant communities and alter ecosystem functioning (Meyerson *et al.* 1999, Lambert *et al.* 2010, Saltonstall *et al.* 2010). Recent studies have reviewed sub-groups of tall grasses such as invasive grasses that dominate aquatic ecosystems (e.g. "large-statured invasive grasses"), and have argued that they are functionally similar and have generalizable impacts related to their competitive nature (Lambert *et al.* 2010).

More broadly, tall-statured grasses are potentially an important functional group in invasion science because (1) established populations of TSGs can cause significant negative ecological impacts (Pagad 2016, Canavan *et al.* 2017b); (2) large height and biomass contribute to specific environmental impacts, e.g. reduction in light availability, changes to fire regimes, and

alteration of nutrient cycles (D'Antonio and Vitousek 1992, Meyerson *et al.* 1999, Brooks *et al.* 2004, Smith *et al.* 2013, Gaertner *et al.* 2014, Visser *et al.* 2016); (3) TSGs occur in grasslands, riparian areas and estuaries, as well as tropical and temperate forests, yet the abiotic and biotic impacts are often similar across ecosystems; (4) TSGs are increasingly cultivated for commercial purposes such as bioenergy production and phytoremediation and therefore present new risks (Mislevy and Fluck 1992, Czakó *et al.* 2005, Heaton *et al.* 2008, Jakob and Zhou 2009, Mirza *et al.* 2010, Chen *et al.* 2015); and (5) TSGs are often dominant components of the vegetation in their native ranges, providing biotic resistance to invasion (including against alien TSGs) (Sheley and James 2010). However, TSGs have not been fully explored as a distinct functional group until now.

Here, we review the usefulness of the TSG functional group for invasion science. We produce a preliminary list of TSGs, and test whether there is a quantitative pattern in the naturalisation of grasses (all TSGs compared to all non-TSG grasses, and for the subgroup of woody bamboo grasses compared to all other grasses). We identify which TSGs have been subject to risk assessments. We also discuss the invasion-science literature associated with TSGs, focussing on how competitive traits associated with increased height can affect the colonisation, invasion, and environmental impacts of alien grasses.

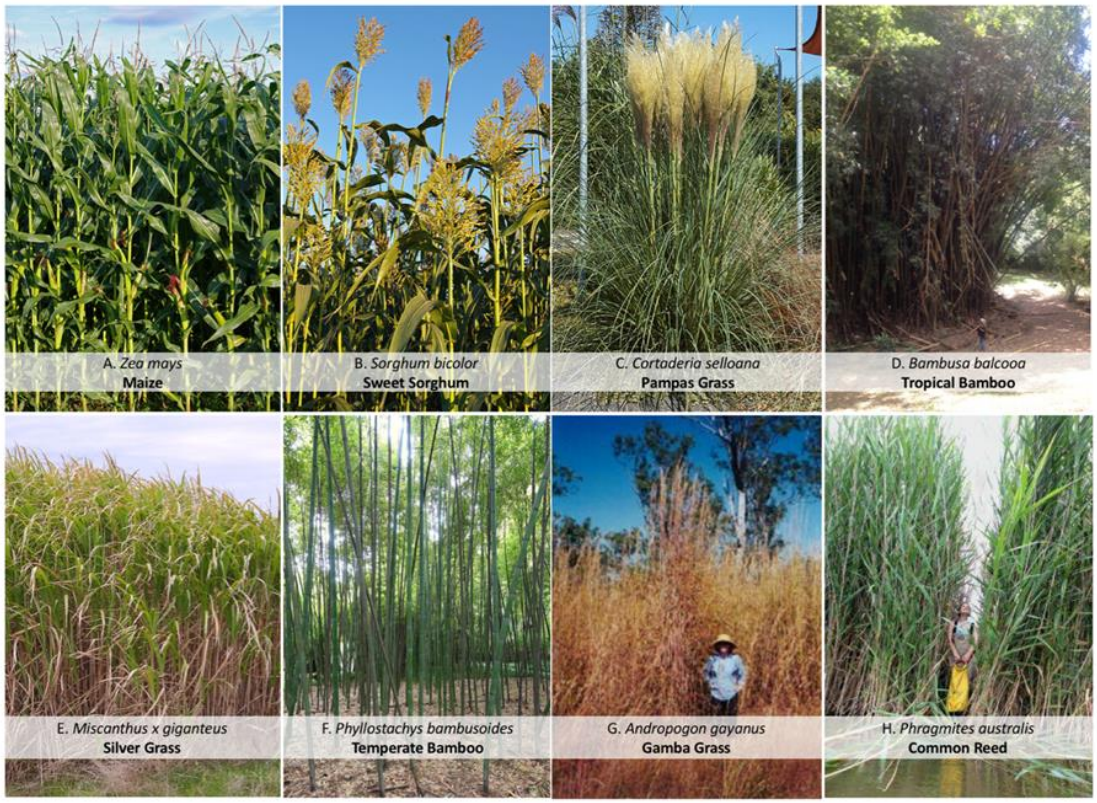


Figure 4.1 Tall-statured grasses (TSGs) come in a variety of forms and occur in a range of different ecosystems (*e.g.* temperate forests- F, dry grasslands- G to tropical wetlands- H). They are useful to humans for food (A & B), ornamental horticulture (C & D), and for biofuels (E & F). Several TSGs are associated with environmental impacts in invaded ranges due to their ability to form monospecific communities that exclude other vegetation types (D, F, G & H). Photographs: Wikimedia Commons (A: Christian Fischer (CC BY-SA 3.0 & CC0); B: Wouter Hagens (CC BY-SA 3.0); E: Bgabrielle (CC-BY-SA-3.0); F: Daderot (CC0)) and other sources (C: Kijktuinen Nunspeet -http://www.kijktuinen.nl); D: Susan Canavan; H: Michigan Technological University).

4.3 METHODS

4.3.1 Defining and creating a list of tall-statured grasses

Height in grasses (defined here as average inflorescence height, as per Kew's *GrassBase*; http://www.kew.org/data/grasses-db.html) varies across three orders of magnitude (2 cm to 20 m; see **Figure** 4.2**).** Efforts to classify vegetation into different height categories include Küchler (1949) and Dansereau (1951) who proposed that "tall herbaceous plants", including grasses, should have an average minimum height of 2 m; Edwards (1983) proposed four height categories for grasses, with tall grasses being 1 m and greater than 2 m to be largest height category; Lambert *et al.* (2010) considered "large-statured invasive grasses" to be greater than 1.5 m in height. There are clearly important ecological correlates for the link between height

and ecological processes, such as competition for light, e.g. light reduction to the soil surface decreases dramatically from 2 m down (Meyerson *et al.* 1999). However, previously proposed height classifications lack a clear ecological justification for their categories, and instead have been developed for practical purposes such as for vegetation inventories, descriptions and surveys (Edwards 1983). We propose 2 m as an ecologically relevant height threshold amongst grasses, and define TSGs as species that are ≥ 2 m. Grasses that maintain a height of ≥ 2 m experience a trade-off between other functional traits. Typical features associated with taller grasses include lignified culms, high growth rates, and abundant biomass (**Table 4.1**). For these reasons, and the common prior use of 2 m as the cut-off, we generated a preliminary list of "tall-statured grasses".

We extracted data on inflorescence height for all grass species from Kew's *GrassBase*. Our list of species was cleaned, updated and corrected; non-bamboo grasses were checked for synonyms using Kew's World Checklist of Selected Plant Families (http://apps.kew.org/wcsp/qsearch.do) and bamboo species were checked using the International Network for Bamboo and Rattan's (INBAR) global checklist (Vorontsova *et al.* 2016). Species that do not maintain their height independently (i.e. those listed as 'climbing', 'scandent', 'rambling', 'prostrate', 'liana' and or 'leaning' [on other vegetation]) were removed from the list of TSGs, and were considered non-TSGs along with shorter species.

4.3.2 Incidence and extent of naturalisation

If increased height is advantageous for colonisation, we expected that TSGs would have higher rates of naturalisation compared to shorter grasses (i.e. non-TSGs). To test for this, we calculated whether: (1) TSGs are more likely to be naturalised in at least one region of the world (what we refer to as 'incidence of naturalisation'); and (2) TSGs are more globally widespread outside their native range (which we refer to as 'extent of naturalization'; see e.g. Razanajatovo *et al.* (2016)). Data from the Global Naturalised Alien Flora (GloNAF) database were used for both analyses. The database covers 843 non-overlapping regions (countries, federal states, islands) covering around 83% of the Earth's land surface.

The effect of stature on the probability of a grass species becoming naturalised could simply mean that TSGs are more likely to be traded because of their ornamental value. To test for this, we used data on plant trade sourced from Dave's Garden Plant Files (http://davesgarden.com/guides/pf), arguably the most comprehensive database of garden plants.

Dave's Garden Plant Files provides an indication of the supply and demand for ornamental plants by private growers in the United States. While it would have been ideal to use quantitative sale and trade data from Dave's Garden as a proxy of propagule pressure, such data were only available for a small subset of species. We therefore confined the analyses to whether or not a species was present in Dave's Garden Plant Files.

When exploring the raw data, it was clear that the vast majority of TSGs were woody bamboos (tribes: Bambuseae and Arundinarieae; **Figure** 4.2). Also, the percentage of TSGs that naturalised was greater than that of non-TSGs for woody bamboos and other grasses (i.e. non-bamboos and non-woody bamboos), although this pattern was not found when pooling all grasses together (a result of inequities in the proportions of the taxa which were TSGs; see **Table S4.4**). For this reason, we conducted the remaining analyses on naturalisation incidence and extent (described below) separately for the set of woody bamboos and for the set of other grasses.

To assess whether naturalisation incidence was higher in TSGs than non-TSGs, we ran generalised linear mixed-effects models with a binomial error distribution (logistic regression), separately for woody bamboos and for other grasses, using the 'lme4' R package (Bates *et al.* 2015). The response variable was status (presence or absence) in the GloNAF database and the predictor variables were whether a species is a TSG or non-TSG, and whether a species was traded or not (as inferred from presence or absence in Dave's Garden Plant Files). To account for phylogenetic non-independence of the species, we included genus (in the case of woody bamboos) and genus nested within tribe (in the case of other grasses) as random factor(s). This also provided an opportunity to test whether the 2 m cut-off was appropriate. We ran similar models with height (standardised to a mean of 0 and standard deviation of 1) as a continuous explanatory variable instead of stature as a binary variable (TSG or non-TSG).

To analyse extent of naturalisation (i.e. number of regions in the GloNAF database) we ran generalised linear mixed-effects models with a negative binomial error distribution, due to high incidence of zeros, separately for woody bamboos and for other grasses, using the 'glmmADMB' R package (Fournier *et al.* 2012). We used the same predictor variables and random factors as in the analysis of naturalisation incidence. Finally, we looked at the global geographic pattern of numbers of naturalised TSGs and of the proportion of TSGs among all naturalised grass species.

4.3.3 Reviewing future risks

To explore the threats of TSGs introduced to new regions, we reviewed risk assessments that have been completed in different parts of the world for our list of TSGs. We did this by searching for primary literature and fact sheets on Scopus, ISI Web of Science and Google Scholar using the keywords specific names of the TSG species/ "tall grass" AND "risk assessment"/ "risk analysis". We collated all the risks assessments and then summarised the species for which assessments have been reported.

4.4 RESULTS

4.4.1 TSG species

From the lists extracted from Kew's GrassBase, we removed 18 species that did not have names matching the World Checklist of Selected Plant Families or INBAR's global 2016 checklist, four unplaced species were kept in the list, and synonyms (n=79) were updated accordingly to reflect current nomenclature. Of the remaining 10,818 grass species for which height data were available, 1,136 species reach heights of 2 m or more, although 207 of these do not maintain their height independently and were classified as non-TSGs. This left 929 species (8.6% of grass species) as TSGs for subsequent analysis (See Online Resource 1 for a complete list of species).

Among TSGs, the vast majority (80.6%) are woody bamboos (tribes Arundinarieae and Bambuseae). The remaining 180 species of TSGs come from 21 tribes in 7 subfamilies (Figure 2), many of which are important reed species, such as Burma reed (*Neyraudia reynaudiana*; Tribe: Triraphideae), common reed (*Phragmites australis*; Tribe: Molinieae), and giant reed *(Arundo donax*; Tribe: Arundineae). Other TSGs include popular horticultural and biofuel species such as pampas grass (*Cortaderia* spp.; Tribe: Danthonieae) and silver grass (*Miscanthus sinensis*; Tribe: Andropogoneae). The TSG group also contains important food crops, in particular maize (*Zea mays*; Tribe: Andropogoneae), pearl millet (*Cenchrus americanus* = *Pennisetum glaucum*; Tribe: Paniceae), sorghum (*Sorghum bicolor*; Tribe: Andropogoneae), and sugarcane (*Saccharum* spp.; Tribe: Andropogoneae)(Fischer *et al.* 2014). With the exception of woody bamboos (Tribes Bambuseae and Arundinariaeae), TSGs are outliers in their respective tribes in terms of height, although the height distribution of all tribes appears to be roughly unimodal (Figure 2).

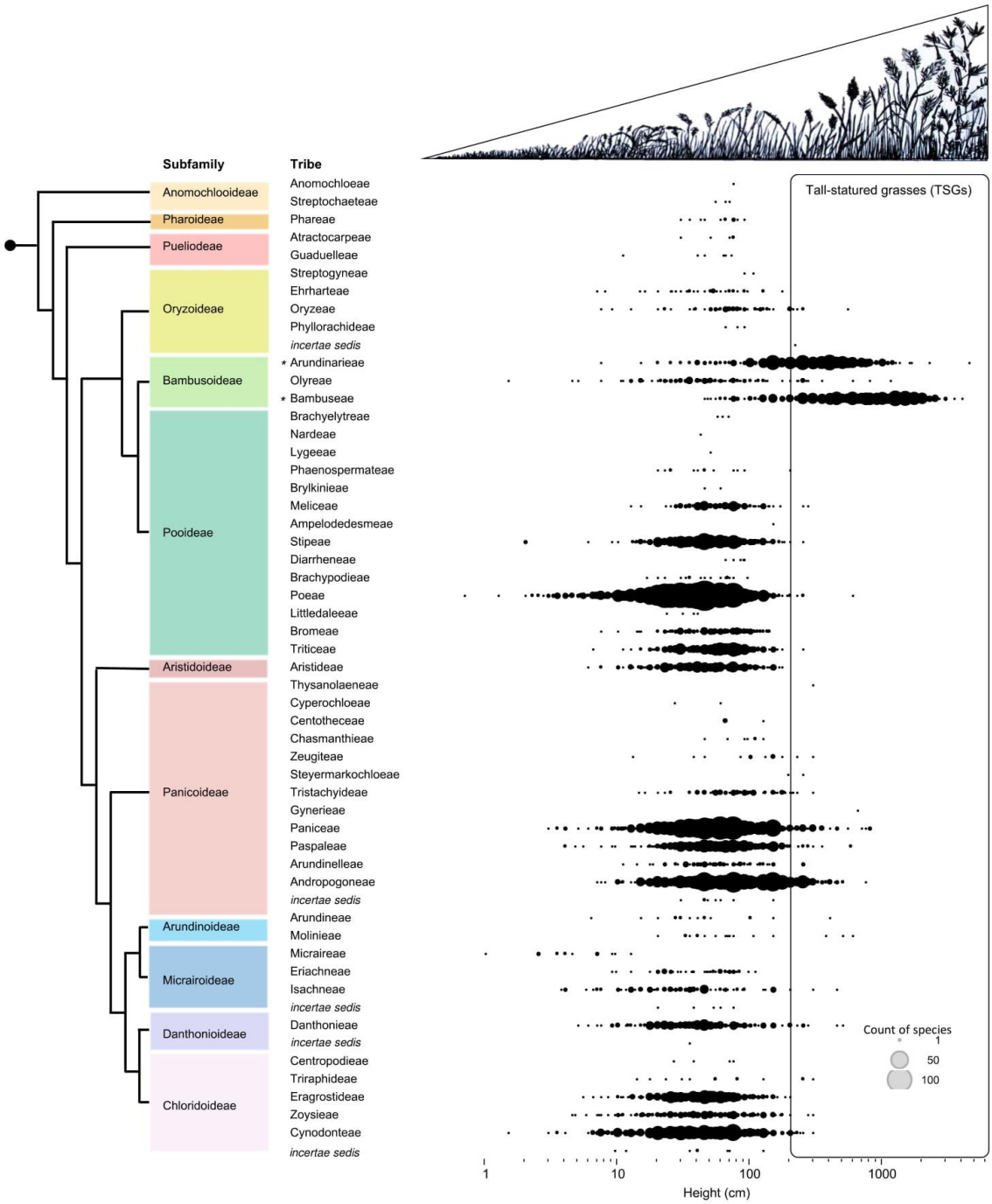


Figure 4.2. Height distribution of grass species in subfamilies and tribes as per Soreng (2015)'s classification of Poaceae. Species within the black-outlined box have average bloom (inflorescence) heights of ≥ 2 m. Note that not all of these taxa are defined in this paper as tall-statured grasses (TSGs) as some taxa do not maintain their height independently (e.g. climbing species). The area of the black circles is proportional to the number of species. Data were retrieved from Kew's GrassBase (http://www.kew.org/data/grasses-db.html) for 10,818 species. Species that are unplaced in a tribe are shown as *incertae sedis* for that subfamily. Woody bamboos (tribes Arundinareae and Bambuseae) are marked with an asterisk. Figure generated using Tableau V 10.0.

4.4.2 Incidences and extent of naturalisation

The GloNAF database lists 1,226 species in the grass family. We found overall a similar percentage of naturalised species among TSGs and among non-TSGs using the 2 m threshold, with 11.4% and 11.3% of species naturalised, respectively (**Figure 4.3**). However, when considering woody bamboos alone, the percentage of naturalised TSGs is more than three times that of non-TSG bamboos, with 7.6% and 2.0% of species, respectively (Fisher's exact test: odds ratio=4.1, 95% confidence interval of 1.9–9.9, $p<0.001$). This is also the case among all other grasses (i.e. excluding woody bamboos), with 27.2% and 11.7%, respectively (Fisher's exact test: odds ratio=2.8, 95% confidence interval of 2.0–4.0, $p<0.001$). The lack of contrast overall between TSGs and non-TSGs is because most TSGs are woody bamboos but fewer woody bamboos than other grasses have naturalised.

Among both woody bamboos and other grasses, species that are traded for ornamental horticulture have naturalised more often than non-horticultural species. Of the 1,233 grass species listed in Dave's Garden Plant Files, 53.4% are naturalised, while only 5.9% of the other 9,585 grass species have naturalised. When the presence of a species in Dave's Garden Plant Files was accounted for in the analysis, tall stature had a significant, positive effect on naturalisation incidence of other grasses (**Table** 4.2**a**). This was not the case for woody bamboos. However, when a similar model was run with height as a continuous variable height had a significant, positive effect on naturalisation incidence for both woody bamboos and other tall grasses (**Table** 4.2**a**).

Of the subset of 1,226 grass species (of all tribes) that have naturalised somewhere, 384 species have naturalised in only one region, whereas some species (e.g. *Eleusine indica*, a non-TSG) have naturalised in up to 309 regions according to the GloNAF database. On average, when considering grasses together, TSGs and non-TSGs have naturalised in similar numbers of regions (Online Resource 4; Wilcoxon test: $W=56274$, $p=0.368$). When considering woody bamboos alone, and while accounting for the strong positive effect of presence in the horticultural trade, the extent of naturalisation was still significantly positively associated with tall stature (**Table** 4.2**b**). Indeed, woody bamboo TSGs have naturalised in up to 101 regions (e.g. *Bambusa vulgaris* being the most widespread species) whereas the 8 non-TSG woody bamboos have

naturalised in at most five regions (**Table S4.1**). However, this effect of stature on naturalisation extent was not found for other grasses **Table 4.2b**).

The regions with the highest number of recorded naturalised alien grasses (irrespective of whether they are a TSG or not) are the southern United States, tropical South America, Hawaii, parts of tropical Africa, Madagascar, Indonesia and New Zealand (**Figure 4.4a**, **Table 4.3**). However, the pattern is strikingly different when using the proportion of TSGs among all naturalised grasses (in part because species richness is affected by differences in sizes of the regions). This relative measure identifies a marked hot spot of TSGs in tropical Africa (especially islands in the Western Indian Ocean), where the proportions in most countries range between 30–70% and even more (**Figure 4.4a).** The Caribbean is a second hotspot (**Figure 4.4b**).

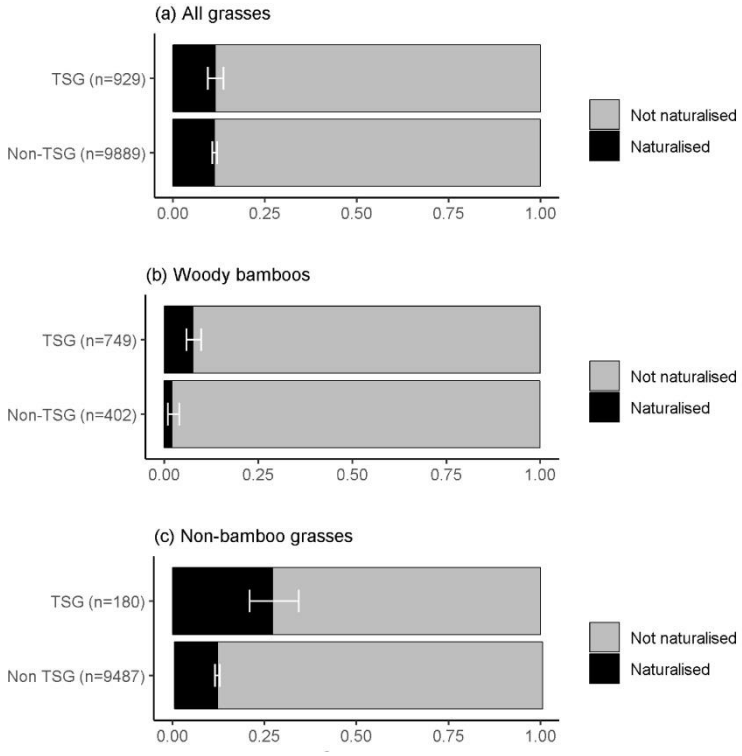


Figure 4.3 Total number of grass species that have naturalised (nat) or not naturalised (not nat) globally, by height group, for (a) all grasses, (b) all grasses excluding woody bamboos (Tribes: Arundinarieae and Bambuseae), and (c) for woody bamboos only. All data were retrieved from the GloNaf database (see Kleunen et al. 2015b). The proportion of tall-statured grasses (TSGs; those that are 2 m in height or greater) and non-TSGs (less than 2 m in height) that have naturalised vary between woody bamboos and

other grasses. There is a very large number of tall-statured non-naturalised bamboos. See Online Resource 4 for the raw data.

4.4.3 Reviewing future risks

We found 127 risk assessments that have been completed for 64 TSG species. Of these, 55 assessments (or 43% and 23 species) had an outcome indicating a high risk for invasion or recommended that further introductions should be rejected in the region evaluated (**Table 4.4**). More than a third (38%) of the risk assessments were conducted on 32 woody bamboo species (all of which are TSGs). However, woody bamboos generally received lower risk scores than other TSGs, with only three risk assessments scoring high risk for two species, and five assessments called for an introduction to be rejected on five species.

The most widely used risk assessment scheme was the Hawaiian Weed Risk Assessment (H-WRA), which has been applied in 60 assessments, followed by the Australian Weed Risk Assessment (A-WRA) with nine assessments. Another 16 variant risk assessment frameworks were used. The following species had the greatest number of completed risk assessments: *Arundo donax* (12), *Miscanthus sinensis* (8), *Cortaderia jubata* (7), *Sorghum bicolor* (7) and *Cortaderia selloana* (7). Based on the results of the risk assessments, the species with a high potential to cause negative impacts were *Arundo donax*, *Cortaderia jubata*, *Echinochloa pyramidalis* and *Phragmites australis* (**Table 4.4**).

Several intended uses for TSGs were identified as generating heightened risk due to the massive propagule pressure associated with such usage: of the risk assessments completed, 37% were for the introduction of ornamental horticulture and food crops species and 28% for biofuels and bioenergy purposes. The purpose of introduction was unspecified in 42% of assessments.

4.5 DISCUSSION

4.5.1 TSG groups with high impact

Woody bamboos (tribes Arundinarieae and Bambuseae) are among the tallest grasses and make up the majority of TSG species (**Figure** 4.2). They have some of the most varied uses of any plant group and are widely used in agroforestry, medicine, food, fodder, ornamentation and, more recently, phytoremediation and bioenergy, perpetuating distribution and cultivation around the world (Soderstrom and Calderon 1979, Farrelly 1984, Liese and Köhl 2015, Canavan *et al.* 2017b). According to Canavan *et al.* (2017b), at least 232 (14%) of all 1,662 bamboo species have been introduced beyond their native range. However, only 12 species are

recorded as invasive (i.e. spreading), fewer than other grass tribes and less than other TSGs. Although they have been widely introduced, bamboos have lower invasion rates but have high levels of environmental impacts in disturbed forests, both in the native and alien range (O'Connor *et al.* 2000, Teixeira and Oatham 2001, Lima *et al.* 2012, Xu *et al.* 2015, Rother *et al.* 2016, Canavan *et al.* 2018b). This is attributed to the high competitive ability of certain bamboo species and their capacity to rapidly colonise open space in disturbed forest canopies and take advantage of available light and resources. Due to their large size and robust stature, they often alter biotic and abiotic processes and compete with trees. The competitive interaction between bamboos and trees is unusual compared to species in other grass tribes. Tall bamboos are usually not perceived as 'invasive' given their low spread rates, but they should receive closer scrutiny with regard to their potentially large impacts on community structure and ecosystem functioning (Canavan *et al.* 2018b). Recognising the dominance of bamboos and managing their biomass is an integral part of landscape management in many forest ecosystems (Suzaki and Nakatsubo 2001, Larpkern *et al.* 2011, Bai *et al.* 2013).

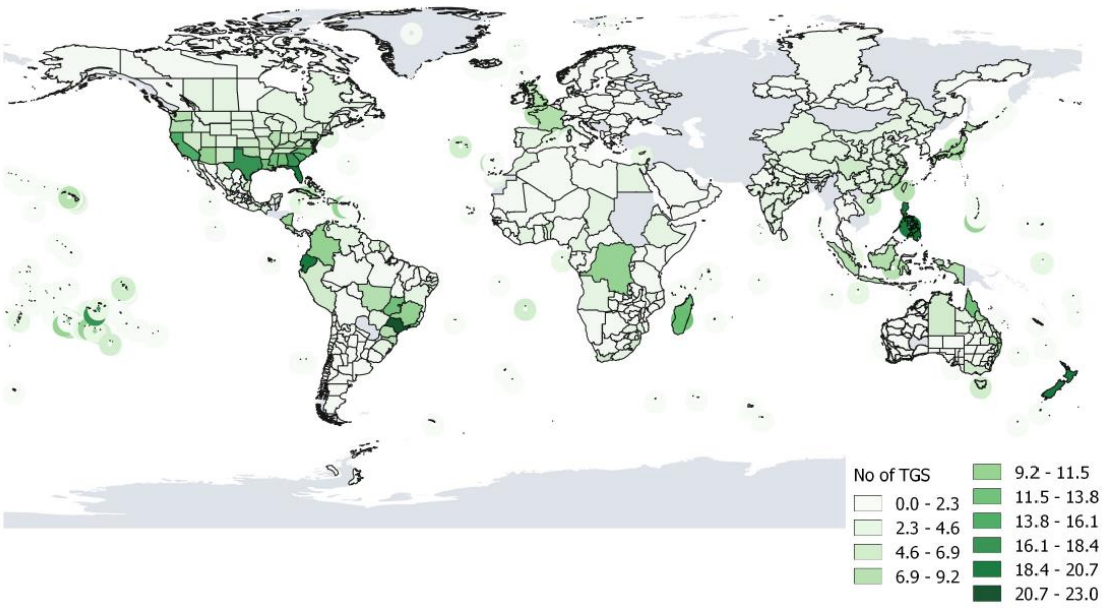
Large reeds form another important subgroup within TSGs and are often the dominant vegetation in riparian, lake and coastal ecosystems. Some of the most notorious invasive plants are reed TSGs; notable species include *Arundo donax* and *Phragmites australis* (Lambert *et al.* 2010). Their presence and growth in ecosystems have important consequences for the structure and composition of their communities (Chambers *et al.* 1999, Meyerson 2000, Meyerson *et al.* 2000, Holmes *et al.* 2005, Richardson *et al.* 2007a, Packer *et al.* 2017). In particular, invasive reeds efficiently exploit space and nutrients, allowing them to take advantage of natural and human-induced disturbances (Meyerson *et al.* 1999, Canavan *et al.* 2018a).

Tall-statured grass species (e.g. *Cortaderia jubata, Cortaderia selloana, Miscanthus sinensis, Panicum virgatum*) are also widely used for ornamental horticulture and bioenergy production. Many species used for this purpose escape from cultivation and spread into natural areas (Lambrinos 2000, Quinn *et al.* 2010, Schnitzler and Essl 2015). Interestingly, food crop TSGs (e.g. maize, sugarcane, pearl millet, sorghum etc.), although widely propagated and very commonly planted as hybrids, tend not to be invaders although they make up a vast component of landscapes altered by humans for agricultural purposes around the world.

4.5.2 Extent and incidence of naturalisation of TSGs

Although we did not find that all models yielded a significant effect of stature, we did show that TSG categorisation is relevant with respect to probability for naturalisation. Specifically, we

found that stature is associated with naturalisation success in grasses, but only when woody bamboos are excluded (**Figure 4.3**). While stature is unlikely the proximate factor driving naturalisation, naturalisation patterns support the notion that being a TSG contributes to invasion potential. In agreement with other studies, we also found that the presence in horticultural trade is an important correlate of both naturalisation incidence and extent (Dehnen-Schmutz *et al.* 2007, van Kleunen *et al.* 2007, Pyšek *et al.* 2010, van Kleunen *et al.* 2018). We also found that TSGs seem to have naturalised more on islands, probably due to the long history of bamboos being widely introduced and cultivated on islands along early trade routes (Canavan et al. 2017b).



b)

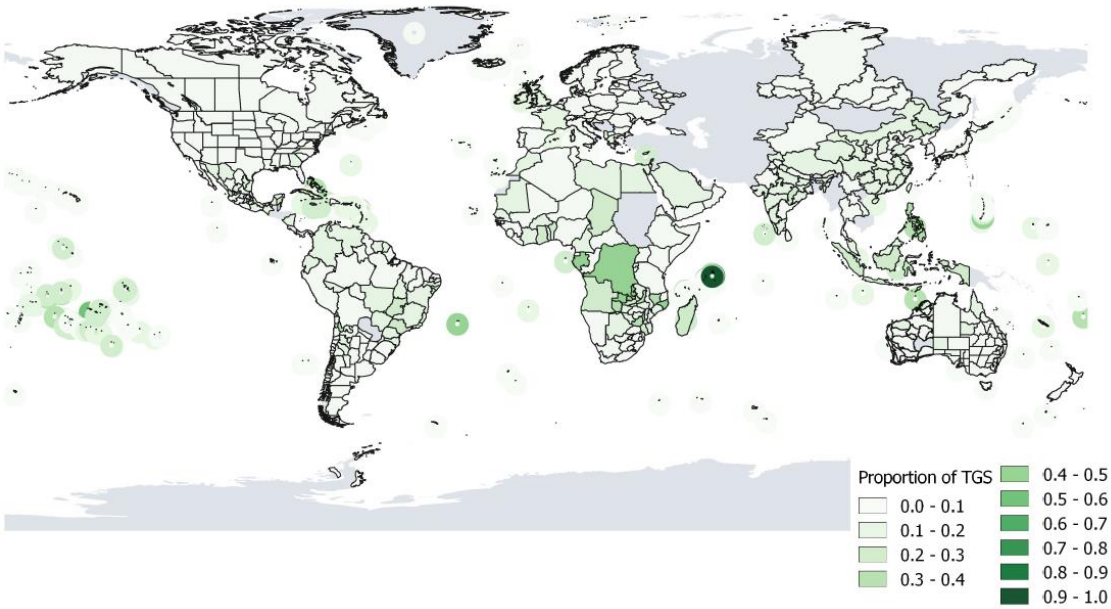


Figure 4.4 Numbers of naturalised tall-statured grass species (top) and their proportions among all naturalised grass species (bottom) in GloNAF regions of the world (see van Kleunen *et al.* (2015) for description of regions and data acquisition). Darker colours indicate a greater number of naturalised TSGs or that naturalised TSGs represent a greater proportion of all naturalised grasses. The occurrence of grasses is indicated by colour intensity.

4.5.3 Competitive features of TSGs

The heights obtained by TSGs (including bamboos) result in unique traits that can confer a competitive advantage over other co-occurring vegetation, including lignified stalks, production of large amounts of biomass (often at a rate faster than woody shrubs and trees; Linder *et al.* (2018)), formation of dense monospecific stands and extensive root and rhizome systems (See **Table 4.1**). Although these traits are not unique to TSGs and are present in other plant groups including shorter grasses, the combination of these traits enables some TSGs to have increased impacts.

Tall-statured grasses are also often the dominant components of the vegetation communities in ecosystems where they occur and thus have a strong effect on ecosystem functioning. As such, they have impacts at different trophic levels when they become invasive (Gordon-Gray and Ward 1971, Onimaru and Yabe 1996, Larpkern *et al.* 2011, Maceda-Veiga *et al.* 2016, Pagad 2016). For example, the accumulation of dead biomass creates thick litter mats that can suppress the growth of emerging plants over time (Haslam 2010, Amougou *et al.* 2012, Rohani *et al.* 2014). The increase of litterfall, and therefore standing biomass, can also lead to changes in fire regimes though increased fuel loads which can inflict ecosystem-level changes, including transformed nutrient cycling and increased susceptibility of the ecosystem to further invasion

(Rieger and Kreager 1989, Dwire and Kauffman 2003, Herrera and Dudley 2003, Brooks *et al.* 2004).

For most TSGs, vegetative growth is both a crucial competitive mechanism and a reproductive strategy for dispersal with tillers, shoots, ramets, rhizomes, stolons or fallen stems forming clonal networks (Wang *et al.* 2017). The connectivity of biomass between stands has many advantages: greater resource acquisition and sharing (de Kroon and Kalliola 1995, Stueffer *et al.* 1996, van Kleunen and Stuefer 1999); allowing invasion into closed canopies or low resource-patches (Welker and Briske 1992, Wang *et al.* 2016); and allowing the storage of resources (Grace 1993). The increased amount of below-ground vegetative biomass of TSGs, compared to shorter grasses and other plants like trees, likely gives populations added resilience to disturbances and provides a greater capacity for energy storage.

Sexual reproduction and seed dispersal is not a prerequisite for the spread of many TSGs (Ahmad *et al.* 2008, Hardion *et al.* 2012, Canavan *et al.* 2017a). Clonal TSGs use stem-derived spacers such as underground rhizomes or above-ground stolons to disperse which can be further aided by anthropogenic activities such as the movement of TSGs for ornamental horticulture and other purposes (SFAPRC 2006, Isagi *et al.* 2016). The ability of some TSGs to successfully colonise a wide variety of environmental gradients and yet have such low genetic diversity may also indicate that other important mechanisms are implicated, such as increased phenotypic plasticity in response to environmental changes (Canavan *et al.* 2017a). Invasive clonal plants like *A. donax* may possess a 'general-purpose-genotype', i.e. a genotype that allows for phenotypic plasticity and thus adaptation to a wide range of conditions (Van Doninck *et al.* 2002). Further, many TSGs have an allopolyploid origin and incorporate high genetic diversity in their genomes (Soltis and Soltis 2000).

Although vegetative growth clearly carries several advantages for the establishment of TSGs, this mode of dispersal alone has limitations. When TSGs can also reproduce sexually they have the added advantage of being able to achieve long-range dispersal independently (e.g. without the need for disturbance or human-facilitation) into adventive ranges. Sexual reproduction also produces genetic diversity and increases the opportunities for naturalisation and eventually adaptation to new habitats and ranges (Colautti and Lau 2015). Increased height can also be a competitive advantage in seed dispersal by wind, as pollen and seeds can travel above the canopy and cover long distances (Thomson *et al.* 2011). A number of TSGs have been found to disperse widely via seed production (Quinn *et al.* 2010, Ecker *et al.* 2015), but can also invade

new ranges through the distribution of seeds (Chambers *et al.* 1999, Belzile *et al.* 2010, McCormick *et al.* 2010, Kettenring *et al.* 2011, Bonnett *et al.* 2014).

4.5.4 Risk of invasion and impacts

We found that a majority of risk assessments that have evaluated TSGs have been for horticultural introductions and more recently for bioenergy projects (Scurlock *et al.* 2000, Blanchard *et al.* 2017, Lieurance *et al.* 2018b). Since TSGs are the grasses most often selected for bioenergy and biofuel production, this usage category will probably continue to drive future introductions from the group (Cousens 2008, Amougou *et al.* 2011, Gordon *et al.* 2011, Hartman *et al.* 2011, Jung *et al.* 2015, Smith *et al.* 2015a, Corneli *et al.* 2016). Potential bioenergy TSG crops tend to receive higher risk scores than TSGs selected for other uses (See appendices). The most commonly mentioned candidates for biofuels include *Arundo donax*, *Cenchrus purpureus* (= *Pennisetum purpureum*), *Miscanthus* × *giganteus* (importantly neither parental species grows to ≥ 2 m, indicating selection for greater height), *Saccharum* spp., as well as *Panicum virgatum*, (although just short of the 2 m threshold). The high risk of biofuel-selected species is in line with previous studies; a comprehensive analysis by Buddenhagen *et al.* (2009) found that biofuel species are two to four times more likely to establish and become invasive than species introduced to Hawaii for other purposes.

An additional risk associated with biofuel and bioenergy crops is the intention to develop more robust and vigorous cultivars through genetic manipulation to produce crops that yield more biomass (Bouton 2007). Many of the selected traits overlap with known weedy attributes, such as: (1) fast growth rates; (2) high seed production; (3) wide range of climatic tolerance; (4) adaptability to a wide range of environmental conditions; and (5) few herbivores, pests and diseases in receiving ecosystems (IUCN 2009, Richardson and Blanchard 2011, Flory *et al.* 2012). In general, the high levels of domestication and breeding of TSGs, both historically and currently, have likely increased invasion risks of some species, as more robust cultivars have been and continue to be developed. Concerns have been expressed that, in general, current risk assessment frameworks and policies are limited in their ability to evaluate subspecies or lower taxa (e.g. cultivars, genotypes) and hybrids (Meffin 2013). For example, a cultivar of a species may perform very differently to the wild type of the species as it occurs in nature. Greater intraspecific diversity of a species has been found to be associated with an increased likelihood of naturalisation or establishment (e.g. South African *Iridaceae* species; van Kleunen *et al.* (2007)) and invasion or spread (e.g. bamboos and lineages of *Phragmites*; further; Meyerson *et al.* (2010), Kettenring *et al.* (2011), Meyerson (2013), Canavan *et al.* (2017a)), highlighting the need for better understanding of intraspecific dynamics. Even natural variations within a species

can be problematic in this regard; this has been the case with *P. australis* where a certain haplotype (Saltonstall 2002) and smaller genome sizes (Pyšek *et al.* 2018) are more invasive than others (e.g. displacement of native haplotypes in North America). Invasive genotypes likely exist within other TSGs and other plant taxa more generally (e.g., *Phalaris arundinacea*; Lavergne and Molofsky (2007)), although they go unrecognised due to the difficulty in identifying intraspecific diversity. Additional criteria are needed to evaluate the invasion risks of subspecific or lower taxa, particularly to keep pace with the increasing selection and breeding of TSGs for biofuel and other uses surrounding high biomass yielding variations.

Table 4.1 Typical features of tall-statured grasses (TSGs) that confer a high likelihood of causing widespread invasions and severe environmental impact.

	Features typical of TSGs	Implications for invasiveness / impact	Example
1. Biomass production	Statured architecture	High light capture, so likely to outcompete shorter vegetation	*Miscanthus sinensis* (Tang *et al.* 1990); *Phragmites australis* (Meyerson *et al.* 2000)
	Fast growth rates	Can outcompete neighbouring species	Bamboos (Montti *et al.* 2014)
	Leaf litter build-up	Suppress growth of neighbouring plants	*Miscanthus* x *giganteus* (Amougou *et al.* 2012); *Phragmites australis* (Haslam 2010, Holdredge and Bertness 2011); *Cortaderia jubata* (Lambrinos 2000); *Cortaderia selloana* (Domènech *et al.* 2006)
2. Biomass accumulation	Chemically distinct leaf litter	Reduced decomposition	*Phragmites australis* (Meyerson *et al.* 2000); *Bambusa* spp. (O'Connor *et al.* 2000)
	Chemically distinct leaf litter	Alter nutrient cycling	*Phragmites australis* (Meyerson *et al.* 2000); *Phyllostachys edulis* (Song *et al.* 2017); *Cortaderia selloana* (Domènech *et al.* 2006)
	Production of large quantities of highly flammable aboveground biomass	Alter the frequency and intensity of fires	*Arundo donax* (Herrera and Dudley 2003, McWilliams 2004, Coffman *et al.* 2010, Lambert *et al.* 2010); bamboo (Jaiswal *et al.* 2002); *Andropogon virginicus*, *Hyparrhenia rufa*, *Melinis minutiflora*, *Schizachyrium condensatum* (Brooks *et al.* 2004); *Andropogon gayanus* (Rossiter *et al.* 2003); *Cortaderia selloana* (Bossard *et al.* 2000)
	Tall plants with seeds held high up	Long range dispersal of seeds	Generally in plants (Thompson *et al.* 1995); specifically for grasses (Linder *et al.* 2018); *Cortaderia selloana* (Drewitz and DiTomaso 2004)
	Dense root systems	Crowd out other vegetation	*Phragmites australis* (Meyerson 2000)
3. Dual reproductive modes	Clonal networks leading to greater resource acquisition	Ability to survive high stress environments	*Gynerium sagittatum* (de Kroon and Kalliola 1995); clonal plants in general (Stueffer *et al.* 1996, van Kleunen and Stuefer 1999)
	Clonal networks leading to colonisation by juvenile ramets into low resource patches are supported by older ones	Ability to colonise stressful environments	*Phyllostachys edulis* (Wang *et al.* 2016)
	High belowground allocation / storage of resources	Ability to survive disturbance and regenerate quickly, out-competing neighbouring vegetation	*Miscanthus* spp. (Amougou *et al.* 2011); *Dendrocalamus strictus* (Singh and Singh 1999)

4. Anthropogenic interest	Use as biofuel	Increased dissemination, propagule pressure, often in large stands in climatically suitable areas close to the natural environment	*Miscanthus x giganteus* (Schnitzler and Essl 2015); *Arundo donax* (Cosentino *et al*. 2006); *Miscanthis sinensis* (Flory *et al*. 2012)
	Use in ornamental horticulture (particularly landscaping)	Increased dissemination, propagule pressure, and multiple foci for potential invasions	*Arundo donax*, *Cortaderia selloana*, *Pennisetum purpureum* (Foxcroft *et al.* 2008); *Cortaderia selloana* (Okada *et al.* 2007); *Miscanthus sinensis* (Dougherty 2013); bamboo (Canavan *et al.* 2017b)

4.5.5 The TSG concept and future directions

While there is no clear break in the height distribution of grasses, TSGs are an important functional group as they cause distinct impacts and raise particular concerns for management and biosecurity. We suggest a number of directions that can be taken with the TSG group including: (1) studying subgroups of TSGs in particular biogeographical realms (e.g. Afrotropic TSGs), or habitat types in which they primarily occur (e.g. riparian, estuarine, or forest TSGs). Understanding the reasons for the differences between woody bamboos and other TSGs would be an important first step; (2) determining why different pathways and the traits selected in TSGs are associated with varying levels of risks. For example, trying to better understand why TSGs selected for biofuels are associated with high-risks, whereas food crops tend to be low-risk; (3) reviewing the importance of TSGs in their native range for resisting invasions. For example, the composition of dominant native grasses have been found to be mediators of invasions as well as important predictors of the ability of a system to resist invasion (Tilman *et al.* 1997, Pokorny *et al.* 2005, Richardson *et al.* 2007b, Young *et al.* 2009, Wang *et al.* 2013); and (4) reviewing whether there is merit in expanding the functional group to encompass tall Poales [order of monocotyledons that include grasses, bromeliads and sedges] more generally, as many sedges and rushes employ similar mechanisms to disrupt and produce ecosystem-level changes through biomass production and accumulation (*e.g.* the removal of invasive *Typha* ×”*glauca* biomass, increased native plant diversity along Great Lake coastal wetlands; Angeloni *et al.* (2006); Farrer and Goldberg (2009); Lishawa *et al.* (2015)).

4.6 CONCLUSION

In summary, we believe that the group of TSGs, including bamboos, are a useful functional group both for invasion science and management and that further research on the group, on both the biological reasons and the socio-economic imperatives that drive invasions, is warranted. Tall-statured grasses also provide an important counter-point to other analyses as to when generalisations can be made in invasion science (Kueffer *et al.* 2013).

Table 4.2 The influence of plant stature and garden use status on global naturalisation of woody bamboos and other grasses. Plant stature was categorical [tall-statured grass (TSG), i.e. ≥ 2 m tall vs. non-TSG, < 2 m] and garden-use status was similarly binary (presence/absence in Dave's Garden Plant Files database; http://davesgarden.com/guides/pf). Global naturalisation was measured as (a) naturalisation incidence outside the native range (expressed as being naturalised in at least one region, yes or no), and (b) naturalisation extent (number of regions where the species is recorded as naturalised). To assess whether naturalisation incidence or naturalisation extent related to stature and to the presence in Dave's Garden database, we ran generalised linear mixed-effects models with a binomial error distribution or a negative binomial error distribution, respectively. To account for phylogenetic non-independence of the species, we included genus (for woody bamboos) or genus nested within tribe (for other grasses) as random factor(s). For naturalisation incidence, we ran similar models with height (standardised to a mean of 0 and standard deviation of 1) as a continuous explanatory variable instead of stature, the results are shown in italics. Note that the group of bamboos refers to species within the Bambuseae and Arundinarieae tribe, and non-bamboo grasses include all other species in the family Poaceae.

	(a) Global naturalisation incidence (yes/no)							
	Woody bamboos (n=1162)				Other grasses (n=9674)			
Explanatory variable	Estimate	SE	z	p	Estimate	SE	Z	P
Intercept	-5.365 *-5.101*	0.533 *0.422*	-10.06 *-12.087*	<0.001 *<0.001*	-3.026 *-3.023*	0.181 *0.187*	-16.74 *-16.15*	<0.001 *<0.001*
Stature (TSG/non-TSG) *Height (continuous)*	0.4803 *0.431*	0.470 *0.143*	1.021 *3.021*	0.307 *0.0025*	0.931 *0.159*	0.242 *0.036*	3.85 *4.37*	<0.001 *<0.001*
Recorded in Dave's Garden (yes/no)	3.843 *3.839*	0.428 *0.427*	8.979 *8.983*	<0.001 *<0.001*	3.204 *3.188*	0.092 *0.092*	34.99 *34.79*	<0.001 *<0.001*
Random factors	Std. Dev.				Std. Dev.			
Genus	0.6864 *0.6854*				0.9504 *0.9491*			
Tribe	-				0.5826 *0.6278*			
	(b) Global naturalisation extent (number of regions where naturalised)							
	Woody bamboos (n=67)				Other grasses (n=1162)			
Explanatory variable	Estimate	SE	z	p	Estimate	SE	Z	P
Intercept	-0.612	0.751	-0.81	0.415	1.583	0.142	11.13	<0.001
Stature (TSG/non-TSG)	1.139	0.511	2.23	0.026	-0.147	0.242	-0.61	0.54
Recorded in Dave's Garden (yes/no)	1.340	0.655	2.05	0.041	1.518	0.080	18.92	<0.001
Random factors	Std. Dev.				Std. Dev.			
Genus	0.3947				0.7103			
Tribe	-				0.4037			

Table 4.3 The twenty most widely distributed tall-statured grass species ranked according to the total number of regions in which they are naturalised. Numbers of regions where naturalised and the region(s) where native (coded as 1) are also shown using TDWG classification (see van Kleunen *et al.* (2015). Source of data: GloNAF (van Kleunen *et al.* 2015).

			Occurrence in regions (number of GloNAF regions)									**Origin**								
Taxon	Height (cm)	Tribe	Total	Africa	Asia (temperate)	Asia (tropical)	Australia	Europe	North America	Pacific Islands	South America	Cultivated	Europe	Africa	Asia (temperate)	Asia (tropical)	Australia	Pacific Islands	North America	South America
Arundo donax	400	Arundineae	220	26	12	33	33	7	46	15	48				1	1				
Pennisetum purpureum	350	Paniceae	175	38	11	37	13	0	23	20	33			1						
Sorghum bicolor	350	Andropogoneae	147	12	2	5	34	8	57	9	20			1						
Pennisetum glaucum	225	Paniceae	132	19	33	33	9	0	21	6	11			1						
Zea mays	250	Andropogoneae	120	18	0	2	2	6	52	14	26								1	1
Saccharum officinarum	450	Andropogoneae	113	23	0	2	5	0	18	34	31					1				
Bambusa vulgaris	1750	Bambuseae	101	23	0	10	4	0	11	25	28				1					
Phragmites australis	375	Arundineae	94	1	0	3	3	0	85	0	2		1	1	1	1	1		1	1
Cortaderia selloana	200	Danthonieae	66	6	1	1	16	15	20	7	0									1
Sorghum almum	260	Andropogoneae	63	0	33	1	19	0	10	0	0									1
Zea mexicana	300	Andropogoneae	41	1	33	2	0	0	4	0	1								1	
Phyllostachys aurea	500	Arundinarieae	39	1	0	1	7	2	15	1	12				1					
Chrysopogon zizanioides	225	Andropogoneae	35	6	6	3	0	0	2	13	5					1				
Sorghum arundinaceum	215	Andropogoneae	33	10	0	0	14	0	0	6	3			1						
Olyra latifolia	230	Olyreae	30	30	0	0	0	0	0	0	0			1					1	1
Schizostachyum glaucifolium	650	Bambuseae	28	0	0	0	0	0	0	28	0							1		
Pseudosasa japonica	400	Arundinarieae	27	5	0	0	1	9	11	0	1	1								
Cortaderia jubata	225	Danthonieae	24	8	0	0	7	0	4	1	4									1
Bambusa multiplex	300	Bambuseae	23	2	8	1	1	0	3	4	4				1					
Saccharum ravennae	275	Andropogoneae	22	0	0	1	0	0	21	0	0		1	1	1	1				

Table 4.4 Risk assessments completed for tall-statured grass species. Number of risk assessments completed (RAs), number of regions evaluated (Reg), and the outcome of the evaluation are shown for each species; low risk (LR), intermediate risk (IR), high risk (HR), reject, evaluate further (EF) and other classification (e.g. prohibit for importation). See supplementary material for a detailed list of all assessments.

Species	Common name	RAs	Reg	Accept	LR	IR	HR	Reject	EF	other
Andropogon bicornis L.	West Indian foxtail grass	1	1				1			
Andropogon gayanus Kunth	Gamba grass	1	1					1		
Arundo donax L.	Giant reed	12	9				2	7		1
Bambusa bambos (L.) Voss	Thorny bamboo	1	1						1	
Bambusa chungii McClure	Emperor's blue bamboo	1	1		1					
Bambusa glaucophylla Widjaja	Malay dwarf bamboo	1	1		1					
Bambusa lako Widjaja	Timor black bamboo	2	1		1				1	
Bambusa multiplex (Lour.) Raeusch. ex Schult.	Chinese dwarf bamboo	3	2	1				1	1	
Bambusa oldhamii Munro	Oldhamii bamboo	2	1	1					1	
Bambusa oliveriana Gamble	Bush bamboo	1	1		1					
Bambusa pervariabilis McClure	Puntingpole bamboo	1	1		1					
Bambusa textilis McClure	Weaver's bamboo	1	1		1					
Bambusa tuldoides Munro	Buddha Belly bamboo	1	1						1	
Bambusa vulgaris Schrad.	Common bamboo	3	3		1				2	
Schizostachyum pergracile (Munro) R.B.Majumdar *(= Cephalostachyum pergracile* Munro)	Tinwa bamboo	1	1		1					
Chimonobambusa quadrangularis (Fenzi) Makino	Square bamboo	1	1					1		
Chrysopogon zizanioides (L.) Roberty	Vetiver grass	4	3	2	1		1			
Cortaderia jubata (Lem.) Stapf	Purple pampas grass	7	3				3	3		1
Cortaderia selloana (Schult.) Aschers. & Graebn.	Silver pampas grass	6	4		1		2	2		1
Cymbopogon martini (Roxb.) W.Watson	Ginger grass, Palmarosa	1	1		1					
Dendrocalamus asper (Schult.) Backer ex K.Heyne	Giant bamboo	2	2		1				1	
Dendrocalamus brandisii (Munro) Kurz	Velvetleaf bamboo	1	1						1	
Dendrocalamus sikkimensis Gamble ex Oliver	Philippine sweet shoot bamboo	1	1		1					
Dendrocalamus strictus (Roxb.) Nees	Male bamboo	1	1						1	
Drepanostachyum falcatum (Nees) P.C.Keng	Blue bamboo	1	1	1						
Drepanostachyum khasianum (Munro) P.C.Keng	Khasia bamboo	1	1		1					
Echinochloa pyramidalis (Lam.) Hitchc. & Chase	Antelope grass	2	1				1			1
Fargesia fungosa T.P.Yi	Chocolate bamboo	1	1		1					
Fargesia nitida (Mitford) Keng f. ex T.P.Yi	Blue Fountain bamboo	1	1	1						
Gigantochloa apus (Schult.) Kurz	Gigantochloa	2	2		1				1	
Gigantochloa atroviolacea E.A.Widjaja	Sweet bamboo, pring legi	1	1		1					
Gigantochloa atter (Hassk.) Kurz	Sweet bamboo	1	1		1					

Gigantochloa robusta Kurz	Robust bamboo	1	1		1						
Guadua angustifolia Kunth	Guadua, Columbian thorny bamboo	1	1						1		
Hymenachne amplexicaulis (Spreng.) Zuloaga	Hymenachne	1	1					1			
Miscanthus floridulus (Labill.) Warb. ex K.Schum. & Lauterb.	Giant miscanthus	1	1				1				
Miscanthus sinensis Andersson	Chinese silvergrass	8	7		1	1		3			3
Miscanthus × giganteus J.M.Greef & Deuter ex Hodk. & Renvoize	Giant miscanthus	3	1	3							
Nastus elatus Holttum	New Guinea edible bamboo	1	1		1						
Neyraudia reynaudiana (Kunth) Keng ex Hitchcock	Burma reed	3	1				2	1			
Otatea acuminate (Munro) C.E.Calderon & T.R.Soderstrom *(=Otatea aztecorum*)	Mexican weeping bamboo	1	1		1						
Cenchrus americanus (L.) Morrone *(=Pennisetum glaucum* (L.) R.Br.)	Pearl millet	1	1		1						
Cenchrus macrourus (Trin.) Morrone *(=Pennisetum macrourum* Trin.)	African feathergrass	1	1					1			
Cenchrus purpureus (Schumach.) Morrone *(=Pennisetum purpureum* Schumach.*)*	Elephant grass	5	3					5			
Phragmites australis (Cav.) Trin. ex Steud.	Common reed	4	3					1			3
Phyllostachys aurea Rivière & C.Rivière	Golden bamboo	4	3				2	1	1		
Phyllostachys aureosulcata McClure	Yellow groove bamboo	1	1						1		
Phyllostachys nigra (Lodd.) Munro	Black	2	2				1	1			
Pseudosasa japonica (Steud.) Makino	Arrow bamboo	1	1					1			
Saccharum arundinaceum Retz.	Plume Grass	1	1	1							
Saccharum officinarum L.	Sugarcane	3	2	2				2			
Saccharum ravennae (L.) Murr.	Ravenna Grass	1	1					1			
Saccharum spontaneum L.	Wild sugarcane	1	1				1				
Schizostachyum brachycladum (Kurz) Kurz	Sacred Bali bamboo	1	1		1						
Schizostachyum glaucifolium (Rupr.) Munro	Hawaiian bamboo	1	1		1						
Sorghum bicolor (L.) Moench	Sweet Sorghum	8	4	2	1		2	1			1
Zea mays L.	Corn	3	2	1					2		

5 Alien bamboos in South Africa: a socio-historical perspective

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Compliance with Ethical Standards:

The necessary ethical clearance (SU-HSD-004196) to conduct the research was obtained from the National Health Research Ethics Committee (NHREC: REC-050411-032) at Stellenbosch University. All ethical standards were adhered to. The relevant local authorities were approached for permission to conduct the research and formal, free, prior and informed consent was obtained from all participants. Anonymity was assured.

5.1 ABSTRACT

Changes in fashions and economic imperatives underlying plant introductions have a profound influence on the movement of species around the world. We explore such socio-historical perspectives of bamboo introductions into South Africa by assessing historical trends through a literature review and determining current human perceptions using a questionnaire distributed via social media. We identify five main phases of introduction and distribution of bamboos in South Africa associated with: (1) the intra-African migration of people; (2) the arrival of Europeans; (3) growth of the agricultural and forestry sectors; (4) small-scale domestic use by landowners; and (5) the rise of the "green economy". Our narrative is built around 26 alien bamboo species (taxa mentioned in the literature which could be linked to currently accepted species). Bamboos were among the first plants introduced to South Africa by European settlers, and they are still used and valued by many landowners, although on a small-scale. Bamboos now create conflicts of interest because they are both valued and perceived to be weeds (the latter particularly by people who do not utilise the plants). The story of bamboo in South Africa provides a rich example of the initial motivations for introductions, the processes of cultural integration, and the emergence of polarized attitudes as species spread and become weedy.

5.2 INTRODUCTION

The domestication of plants and animals, and their transfer around the world has been instrumental in the development of complex societies (Crosby 1972, Diamond 1997). The expansion of agriculture, including the cultivation of food crops and commercial forestry, has allowed humans to expand and thrive in new regions (Gupta 2004). Examining the socio-historical context of intentional plant introductions can reveal how changes in fashions/desirability and economic imperatives have influenced which species humans have moved around the world. Perceptions and attitudes relating to the value of species often change over time and many intentionally introduced species of plants lose their value over time. This is especially the case when introduced plant populations spread beyond sites of introduction and cultivation and become invasive (Starfinger *et al.* 2003, van Wilgen and Richardson 2014).

The values attached to alien plants by people, strongly influences the likelihood of preventing introductions of species that pose a high risk of becoming invasive. Values also shape the options for management interventions (Lindemann-Matthies 2016). For example, species viewed as desirable are more likely to be propagated and disseminated by people whereas those that are viewed negatively or with indifference are less likely to be distributed intentionally; there is usually greater support for management of species in the latter categories (Zengeya *et al.* 2017). Perceptions also determine the level of stakeholder engagement that is needed to manage "conflict of interest species" – those perceived to have benefits and costs by different groups of people (Novoa *et al.* 2018). For example, Lindemann-Matthies (2016) found that in Switzerland when alien plants are viewed as beautiful by the public there is less willingness to support the management of those species, even when people are informed of their negative environmental and economic impacts. Other influences on people's perceptions of non-native plants include the historic context surrounding the introduction of a species and the timeline, as many species become integrated into culture and livelihoods, e.g. the prickly pear in South Africa (Shackleton *et al.* 2007).

Bamboos are a large group of grasses (c.1600 species) that are particularly important culturally and economically in Asia, which has the highest number of native bamboo species (Canavan *et al.* 2017b). Bamboos have been cultivated and widely used for millennia in China (Li and Kobayashi 2004). There is a growing demand for bamboo products globally, and the commercial cultivation of Asian bamboo species has been expanding to new regions. In South Africa, for example, the commercialization of bamboo species (mostly Asian taxa) has been

proposed as a contribution to the 'green development' of the economy by providing a potential source of renewable bioenergy, among other uses. Scheba *et al.* (2017) identified various emerging stakeholders in South Africa involved in cultivating bamboo who are promoting the introduction of new species, and encouraging more widespread cultivation.

The introduction of bamboos to South Africa has a long history (**Figure 5.1**). Bamboos are one of the earliest plant introductions to South Africa by European settlers (c. 1653) (Claassens and Pretorius 2004). Bamboos are now naturalized across the country, growing around rural homesteads and as screens in urban gardens. However, several species of bamboo are known to be invasive in other parts of the world, and some cause considerable environmental impacts, especially in forest habitats (Canavan *et al.* 2017b, Canavan *et al.* 2018b). The growing interest in bamboo has increased the area under bamboo cultivation in South Africa and has incentivised the introduction of new species to the country. Given that there are species that pose a risk of becoming invasive and causing environmental and economic impacts, there might be unforeseen consequences associated with the current popularisation of bamboos in South Africa.

In several parts of the world the perceived value of bamboos has changed over time when populations stopped being managed and/or became invasive. For example, *Phyllostachys edulis*, a temperate bamboo from China, was introduced to Japan in 1736 as a non-timber forestry plant (Suzuki 1978). A change in land-use and the decline of the domestic bamboo industry led to the abandonment of plantations and the subsequent spread of bamboo into neighbouring forests. This species (and another, *P. bambusoides*) are now perceived as problematic in Japan (Fukushima *et al.* 2014, Takano *et al.* 2017, Wu *et al.* 2018).

Although bamboos have had a long history of introductions around the world, have high usage potential, and are increasingly considered as potential invaders (Canavan *et al.* 2017b, Canavan *et al.* 2018b) few reports exist, on the importance of the socio-historical aspects of bamboos and the links between such factors and invasions. Due to the long history and rapid increase in interest in growing bamboos in South Africa, conflicts of interest may emerge. Such conflicts of interest have thwarted effective management in other plant groups in South Africa (e.g. van Wilgen and Richardson (2012); Novoa *et al.* (2016)) and timeous inventions are needed to prevent similar problems with bamboos. Therefore, in this study we (1) present a historical narrative of the introduction of bamboos to South Africa; and (2) assess the current human perceptions of bamboos in South Africa as useful plants and as weeds.

5.3 METHODS

5.3.1 Literature search of historical records

An online search was done to compile a database of historical literature addressing bamboos introductions in South Africa with the aims of (1) compiling a list of introduced species; (2) documenting original localities of plantings; (3) assessing reasons for introduction; and (4) documenting the dates of introduction. We used the Sabinet database (https://www.sabinet.co.za), an online resource for southern African publications (including almost 500 African journals) which includes an extensive collection of digitised historical archive material. Google Scholar and Google were also used, although they yielded few results. We searched the general terms *bamboo* or *bamboes* [Afrikaans] and the names of common genera (e.g. *Bambusa*, *Dendrocalamus* and *Phyllostachys*) in combination with "*South Africa*". Additional publications were located through snowballing of reference lists.

5.3.2 Questionnaire

We compiled an online questionnaire (using Google Forms; Link to form: https://goo.gl/forms/uVKUL9LCUzl3BZK53 or see **Table S5.3**) directed at landowners or residents in South Africa with bamboos on their property. The questionnaire was developed to understand the perceptions and the current uses, if any, of bamboos. It was circulated by intermittent posting during May 2017 on South African groups (see **Table S5.1**) on social media (Facebook), where users could access a link to the survey and complete it voluntarily. We posted the questionnaire to a total of 50 Facebook groups and the questionnaire was further shared independently by Facebook users 32 times on personal accounts and groups. Some users shared the questionnaire via email and through conservancy newsletters. In this study we present the results of the following questions: When was the bamboo planted? How much space does the bamboo occupy currently? Would you consider the bamboo a weed? How often do you use the bamboo? Have you attempted to remove the bamboo population? Has the bamboo spread more than 2 meters in a year? Respondents were also asked to list the ways in which they use the bamboos, and the ways in which they have had problems with it.

Bamboos are commonly classified into two groups: (1) temperate species with leptomorph rhizomes ("running" species); and (2) tropical species with pachymorph rhizomes ("clumping" species) (Makita 1998). As running or clumping species disperse infrequently via seeds, rhizome expansion is the main mode of spread. Lieurance *et al.* (2018a) reported that running

species scored higher than clumping species in risk assessments for invasive potential in the continental United States. We therefore expected that the growth form (running or clumping) would influence the perceptions of landowners on the weediness of bamboos. We asked respondents to identify whether they had running or clumping species by providing photographs of examples of the most common species found in South Africa (the features of the two groups are easily distinguishable). Some respondents had more than one type of bamboo and some did not specify the type (we grouped these as "unspecified"). It would have been preferable to identify plants to the species level but this was not possible due to limitations of an online survey and our inability to verify all identifications provided by respondents.

We used a two-way chi-square test to compare responses with categorical answers between the three types of bamboo (running, clumping and unspecified), for six questions (**Figure 5.3**). We used a Wilcoxon signed-rank test to compare the mean scores of whether bamboo is perceived as useful or problematic according to respondents (**Figure 5.4**). All analyses and data visualization were done using R 3.4.3 (R Core Team 2017).

Table 5.1 Bamboo species recorded as introduced to South Africa based on the literature, including the earliest record of introduction (ERO) formally reported as determined by Visser *et al.* (2017) and the references specified. Synonyms have been corrected according to The Plant List (www.theplantlist.org) in March 2018, with the original names as per the source shown in brackets. Where the authority was not given we used the one given in The Plant List for the accepted species.

Species	ERO	Reference
Bambusa balcooa Roxb.	1866	(Glen 2002, Visser *et al.* 2017)
Bambusa bambos (L.) Voss *(=Bambusa arundinacea; Bambusa spinosa*)	1823	(Legat 1905, Glen 2002, Visser *et al.* 2017)
Bambusa flexuosa Munro	1910	(Reid 1910)
**Bambusa guilioe*	1910	(Reid 1910)
Bambusa multiplex (Lour.) Raeusch. ex Schult. (=*Bambusa nana*)	1972	(Legat 1905, Glen 2002, Visser *et al.* 2017)
Bambusa oldhamii Munro	1945	(Glen 2002, Visser *et al.* 2017)
Bambusa polymorpha Munro (=*Arundarbor polymorpha*)	1992	(Glen 2002, Visser *et al.* 2017)
**Bambusa simoin*	-	(Reid 1910)
**Bambusa swochiki*	-	(Reid 1910)
Bambusa textilis McClure	-	(Glen 2002)
Bambusa vulgaris Schrad. (=*Bambusa mitis*)	1905	(Legat 1905, Reid 1910, Glen 2002, Visser *et al.* 2017)
**Bambusa variegata*	-	
Dendrocalamus asper (Schult.) Backer (=*Gigantochloa aspera*)	1905	(Legat 1905)
Dendrocalamus giganteus Munro	1878	(Legat 1905, Glen 2002, Visser *et al.* 2017)
Dendrocalamus latiflorus Munro	-	(Glen 2002)
Dendrocalamus membranaceus Munro	1910	(Reid 1910)
**Dendrocalamus siamensis*	-	(Legat 1905)
Dendrocalamus strictus (Roxb.) Nees	1905	(Legat 1905, Reid 1910, Glen 2002, Visser *et al.* 2017)
*Drepanostachyum falcatum (*Nees) Keng f.	-	(Glen 2002)
Himalayacalamus hookerianus (Munro) Stapleton (=*Arundinaria hookeriana*)	1905	(Legat 1905)
*Melocanna baccifera (*Roxb.) Kurz (=*Melocanna bambusoides*)	1905	(Legat 1905)
**Ochlandra rumphiana*	-	(Legat 1905)
*Ochlandra scriptoria (*Dennst.) C.E.C.Fisch (=*Ochlandra rheedii*)	1905	(Legat 1905)
**Ochlandra spinosa*	-	(Legat 1905)

†*Olyra latifolia* L.	1895	(Glen 2002, Visser *et al.* 2017)
Oxytenanthera abyssinica (A.Rich.) Munro	1952	(Glen 2002, Visser *et al.* 2017)
Phyllostachys aurea Rivière & C.Rivière	1927	(Glen 2002, Visser *et al.* 2017)
Phyllostachys nigra (Lodd. ex Lindl.) Munro	1932	(Visser *et al.* 2017)
*Phyllostachys viridiglaucescens (*Carrière) Rivière & C.Rivière (=*Bambusa viridiglaucesens*)	1910	(Reid 1910)
Pleioblastus fortunei (Van Houtte) Nakai (=*Bambusa fortunei*)	1910	(Reid 1910)
Pleioblastus simonii (Carrière) Nakai (=*Bambusa simonii & Bambusa mitake*)	1910	(Reid 1910, Glen 2002)
Pseudosasa hindsii (Munro) Nakai	-	(Glen 2002)
Schizostachyum dullooa (Gamble) R.B.Majumdar (=*Teinostachyum dullooa*)	1905	(Legat 1905)
Thyrsostachys siamensis Gamble	1905	(Legat 1905)

* Unknown species
† The native range of this in Africa is not clear; we follow Visser *et al.* (2017) in considering the species to be alien to South Africa.

5.4 RESULTS AND DISCUSSION

5.4.1 Historical narrative of the introduction and use of bamboos in South Africa

Our literature search found 40 papers that referenced bamboos in South Africa in line with our criteria (see **Table S5.2**). Twenty-four papers referred to the usage of bamboo, seven mentioned aspects of cultivation, five discussed the history of introduction, and four more recent papers provided inventories of naturalised and invasive species. Most references (75%) used the general term ‘bamboo’ (or *bamboes* [Afrikaans]) and only 10 papers identified the species. Of those that did mention a species, 28% were synonyms or unknown species (**Table 5.1**). In total, we found evidence of 34 species, primarily Asian taxa, having been introduced to South Africa (**Table 5.1**). The list includes 26 taxa that could be linked to currently accepted bamboo species (7 additional species names used in the literature could not be linked to currently accepted names, including known synonyms). Of the 26 species, 18 species were included in Visser *et al.* (2017) list of alien grasses in South Africa. The use of bamboo by foresters has provided the best records on the importation of species, whereas references to bamboos from other periods were less clear regarding the species that were introduced.

Most plant introductions to South Africa and elsewhere are associated with particular sectors of society e.g. *Acacia*, *Eucalyptus* and *Pinus* species with foresters (van Wilgen and Richardson 2014), or *Prosopis* with rural farmers (Shackleton *et al.* 2015). In India, where many bamboos are native, they are commonly referred to as "poor man's timber" due to their use among subsistence farmers (Singh 2008). The historical literature shows that this was not the case in South Africa, where bamboos have been valued by people across sectors, social classes and demographic groups (**Figure 5.1** and **Figure 5.2**). There have been multiple surges of bamboo introductions, each associated with different species and different groups of people. These include: (1) the early intercontinental migration of people; (2) the arrival of the first European settlers; (3) the growth of the agricultural and forestry sector; (4) the general domestic use on farms and homesteads and, most recently; and (5) the rise of the green economy. We discuss each of these periods of introduction and distribution that are related to major events in South African history (**Figure 5.1**).

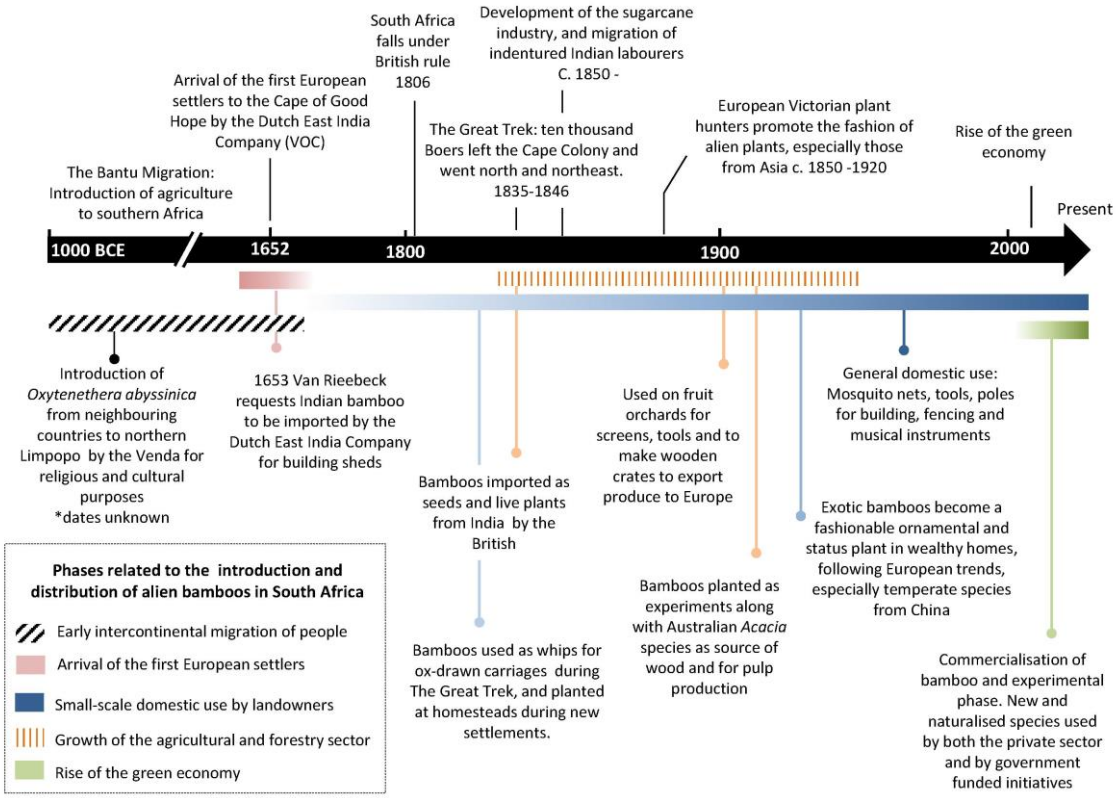

Figure 5.1 Timeline of important historical events (above) related to the introduction, distribution and use of bamboo species in South Africa (below). *Timeline not to scale.

5.4.1.1 Early inter-continental migration of people

The earliest introduction of bamboos to South Africa is thought to have been made by the ancestors of the Venda people. The Venda migrated from Zimbabwe and the East African Rift Valley during the last of the Bantu expansions (c. 1000 BC to c. AD 500) where they settled in the far north-eastern corner of South Africa, now the Limpopo province. They introduced the East African bamboo *Oxytenanthera abyssinica* (A. Rich.), regionally known as 'holy Venda bamboo' or "musununu", to South Africa. As the name suggests, the bamboo is valued for traditional holy ceremonies and is also used to make musical instruments – such as flutes (Stayt and Hoernle 1931, Blacking 1962, Netshlungani *et al.* 1981). The bamboo has been reported to grow in only one sacred grove at Tshuaulu, and as the bamboo is highly revered among the Venda, the remaining populations are protected (Blacking 1969, Harris *et al.* 2015). This has led to the traditional flutes being replaced with modern materials (e.g. hosepipes, metal tubing etc.). Native reeds are also used to make flutes but unlike the musununu bamboo flutes which are heptatonic, they are pentatonic, and therefore not interchangeable (Blacking 1962). In the early 20th century, the bamboo was also reported to be used for arrow shafts for hunting, and to provide splints for bone fractures (Stayt and Hoernle 1931).

Although *O. abyssinica* is thought to be the earliest introduction of bamboo, another herbaceous bamboo species, *Olyra latifolia*, was introduced to South Africa from further north of the continent (Clayton and Renvoize 1986, Soderstrom and Zuloaga 1989, Henderson 2007). It is not known when and how *O. latifolia* was introduced to South Africa. It is possible that the introduction of this species pre-dated the arrival of *O. abyssinica* with early migrations. The herbaceous culms of *O. latifolia* are thin and flexible and cannot be used like other bamboos and are less valuable. However, the plant is used in other parts of Africa. For example, the hollow stems are used to make straws and tools for spinning in Ethiopia (Bekele-Tesemma 2007), in Central and West Africa the leaves are used in various medicines, and in the Central African Republic culms are used for arrow shafts (Burkhill 1994).

5.4.1.2 The arrival of the first Europeans

When the Dutch East India Company (VOC) started the first European settlement at the Cape of Good Hope, they brought a consignment of plants for cultivation (Pooley 2009). Bamboos were some of the first plants introduced in 1653 by the VOC (Spilhaus 1966). Jan van Riebeeck, the Dutch colonial administrator, requested seeds and plants to be imported from India to grow as future building material for garden sheds: "Bamboo plants and seeds will be useful in many

ways as there is no suitable forest here to make anything … Would like to have some old bamboos to be used for little *pondoks* [=basic hut or shelter] on the land." (Leibbrandt 1900, Spilhaus 1966). Letters from van Riebeeck indicated that not all tropical plants (such as pineapple and coconuts) fared well in the Mediterranean-climate conditions of the Cape, but he remarked on how well bamboos grew in gardens (Claassens and Pretorius 2004). Bamboo provided building material, but was also used for food (Claassens and Pretorius 2004). One of the first references in South Africa for *atjar* (or achaar), a spiced pickle condiment introduced by Malay slaves, mentions the fact that bamboo shoots were used (Kolb 1726). *Atjar* is still popular in South African cuisine, although bamboo shoots are now rarely added.

The general usefulness of bamboo continued in the Cape in the following century. During the travels of Thunberg (1795) bamboos were categorised as "useful for the purpose of domestic and rural-economy" for various tools and utensils. Unfortunately, early records mention no particular species, but only note that the bamboos were of Indian origin. In fact, it was during this time that the word 'bamboo' was born, originating from the Dutch word which was adapted from Malay 'mambu' (where bamboos were most likely sourced by the VOC). The influence of the early Dutch traders in disseminating bamboos to other regions extends beyond the Cape; there is a legacy of naturalised populations (most commonly *Bambusa vulgaris*) that still exist on tropical islands along early trade routes (Canavan *et al.* 2017b).

5.4.1.3 The growth of agricultural and forestry sector

During the mid-19th to the early 20th century the British, who now occupied much of South Africa, were expanding the agricultural sector considerably to supply other colonies. To meet the high labour demands, particularly to develop the sugarcane industry (1860 onwards) in what is now KwaZulu-Natal, indentured labourers were brought from India. Bamboos were also imported from India during this time (Legat 1905). They were planted by sugarcane farmers as windbreaks, but also by Indian labourers around homes. Bamboos were an important resource for the Indian community as they provided materials for building and making tools, and they were also used for religious ceremonies. In Muslim communities, bamboos were used to build miniature mausoleums called tazzias for the Muharram festival as early as the 1900s (Vahed 2009). Among the Hindu population, player-flags ("Jhandi") were constructed using bamboo poles to send messages to a Hindu god (Kearney 1999). It is suggested that the infamous "Bamboo Square" (1873-1903), the first settlement of marginalised people in Durban that had a prevalence of Indian, Chinese and Malay inhabitants, received its name from the bamboo prayer flags that would have been erected by the community (Kearney 2002). Prayer flags are still

made today using bamboo poles, especially in the Tongaat region of KwaZulu-Natal. The highest density of bamboo populations (*Bambusa balcooa* and *B. vulgaris*) in South Africa occurs in KwaZulu-Natal.

As in the sugarcane industry, the fruit-growing industry also employed indentured Indians in the second half of the 19th century and bamboo became a useful resource in fruit orchards. There was a shortage of timber, and packing fruit in wooden crates for export was costly. Eventually, fast-growing bamboo was used; culms were processed to construct crates for not only fruit but other crops and for packing harvested tobacco (Ergates 1906, Davies 1910, Fletcher 1925). These were expertly constructed by Indian labourers who were experienced in using bamboo (**Figure 5.2G**) (Ergates 1902, 1906). Bamboos were also used for windbreaks and to make tools such as axe handles and ladders (Ergates 1902, du Plessis 1939).

In the early 20th century, foresters became interested in the commercial cultivation of bamboo as a potential source of woody biomass (Bennett 2011). Bamboo plantations were established alongside Australian acacias in the Zululand district (Davies 1908). Bamboos were also planted in Emakhazeni in Mpumalanga for use in hut building and as a general construction material in rural areas (Sawer 1909). In Barberton, Mpumalanga, seeds of *Dendrocalamus strictus* from India were successfully grown in the government nursery (Davies 1910). Cuttings were raised by the Forestry Division and were distributed around the country. Bamboo proved to be well-adapted to the climate of the Lowveld region, which includes much of the Mpumalanga and KwaZulu-Natal provinces and parts of Swaziland (Taylor 1910). During this time there was also experimental paper manufacturing using bamboo (Exchange Reviews 1908). How extensively bamboo was planted during this time remains unknown.

5.4.1.4 The domestic use of bamboos

Bamboo has been an important resource on farms and homesteads across South Africa for small-scale uses. Clementz (1931) proposed it to be planted along streams and river ways to fight erosion on farms, but also to provide poles for hut building and as food for cattle (Cleghorne 1931). Bamboo culms were used to construct mosquito nets (Simpson 1904), tools (Ergates 1902, Olivier 1938, du Plessis 1939), poles for building and fencing (Ergates 1906), garden trellises (Terry 1927, Esselen 1930), and musical instruments (Liengme 1983). Zulu communities use bamboos to stabilise raised graves and to decorate pottery (*S. Canavan, pers. obs.*). In some areas of the rural KwaZulu-Natal, the traditional wattle and daub huts are built with bamboos instead of wattle (*Acacia* spp.) as there are many naturalised populations (*S.*

Canavan, pers. obs.). This type of building construction has also been noted among the Venda (Magwede *et al.* 2018).

Bamboos have been, and still are, widely used as ornamental horticultural plants in gardens. They became particularly fashionable as garden subjects in the 19th century through the influence of European plant collectors during the Victorian era. During this time The Royal Botanic Gardens at Kew, UK, received and cultivated many temperate bamboo varieties from Asia (Townsend 2013). For example, William Keit, a German botanist with close connections with Kew, traded and distributed alien species for horticulture in South Africa (McCracken 1986). He planted bamboo along roadsides and in the Durban Botanical Gardens as part of his efforts to beautify the city.

5.4.1.5 Into the future: The rise of the green economy

The most recent chapter of the bamboo story has been spurred by a trend towards improved sustainability in industry and agriculture over the past decade. Specifically there has been the rise of the green economy concept which promotes economic activity with lower environmental impact (Department of Environmental Affairs 2007). This has led to the exploration of alternative species that are suited for modern uses such as biofuels, bioenergy, phytoremediation and rehabilitation of mines (see Mothapo (2017). Bamboos have been in the limelight for meeting such criteria.

Scheba *et al.* (2017) reviewed the potential use of bamboo for 'green development' in South Africa, and identified numerous stakeholder groups who were experimenting and distributing bamboos for these purposes: (1) nursery and tissue-culture sellers; (2) commercial growers; (3) specialised retailers; (4) government; and (5) consultants. This has led to the importation of many new undocumented species (pers. Comm. Joubert Roux) for experimentation, including taxa from regions outside Asia such as the Neotropics. New plantations, however, are predominantly planted with species that have already naturalised in South Africa such as *Bambusa balcooa* and *B. vulgaris*. The further development of the bamboo industry faces multiple challenges, including land conflicts, complex governance arrangements, and limitations in the technology available for processing raw bamboo into value-added products (Scheba *et al.* 2017). It is therefore still unclear what impact (positive or negative) this trend may have, and whether the bamboo market in South Africa will become the burgeoning industry suggested in some reports.

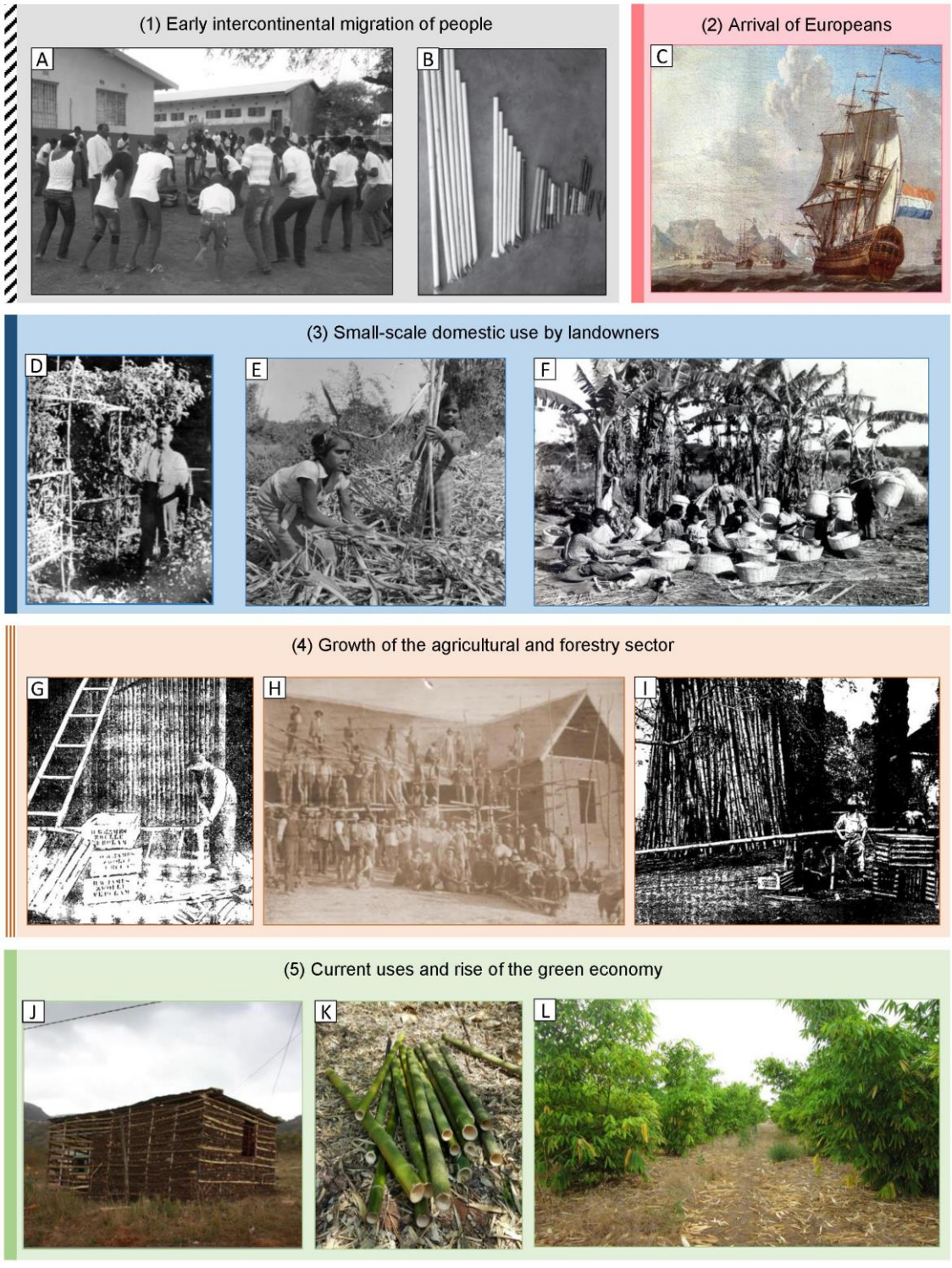

Figure 5.2 Historical photographs showing the cultivation and use of alien bamboos in South Africa grouped by the five phases of introduction and distribution (See Figure 5.1). (A & B) Venda school children practice the *Tshikona* dance, which traditionally includes music played with flutes made from introduced *Oxytenethera* bamboo (B) (source: Tracey and Gumboreshumba (2013).(C) The arrival of the Dutch East India Company to the Cape of Good Hope brought a consignment of plants for cultivation including tropical bamboos from India (source: http://www.voc-kaap.org). (D) Tomatoes trellised with bamboo poles for the "tallest tomato plant" contest in Ficksburg, Free State, circa 1920s (source: Felix

Sorman, personal archive). (E) Children harvesting sugarcane on the KwaZulu-Natal's North Coast in 1957; bamboo windbreak in the background (Photo: Ranjith Kally). (F) Basket making from split bamboos by Indian labourers in c.1909 in Umzinto, KwaZulu-Natal (Source: Collection of The 1860 Heritage Centre).(H) the building of an early mission near Modjadjiskloof using bamboo and *Eucalyptus* poles as scaffolding c. 1890s (source: Felix Sorman, personal archive). (I & F) The construction of bamboo boxes for transporting fruit to Europe, KwaZulu-Natal (Ergates 1902, 1906). A house built with bamboo and daub in rural Zululand, KZN (Photo: Susan Canavan). Harvested bamboo culms from a naturalised roadside population, Limpopo (Photo: Susan Canavan). An experimental plantation of multiple species of bamboo in Vredendal, Western Cape (Source: Susan Canavan).

5.4.2 Current perceptions

Similar to historical uses within gardening and agriculture, the results of the questionnaire indicate that the small-scale use of bamboo in a domestic setting is continuing. In total, 83 respondents completed the questionnaire (3 responses were excluded; 2 were incomplete or incorrectly completed, and one misclassified reeds as bamboos). More than a third (35%; n=28) of respondents (or a relative) had actively planted the bamboo, showing that there is still a desire to propagate and distribute bamboos. Eighty-five percent (n=69) of questionnaires were completed by the owner, tenant, or neighbour of properties of private land whereas 10% (n=8) of respondents related to commercial, business, or public works land, with the questionnaires completed by either the owner, an employee, volunteer or local resident. The majority of respondents had 'inherited' bamboo on their land, but 36% (n=29) did not know who had planted the bamboo or whether it had been planted by previous landowners or tenants. A surprisingly high number of respondents (26%; n=21) reported that the presence of bamboo on their land was the result of invasion from a neighbouring property.

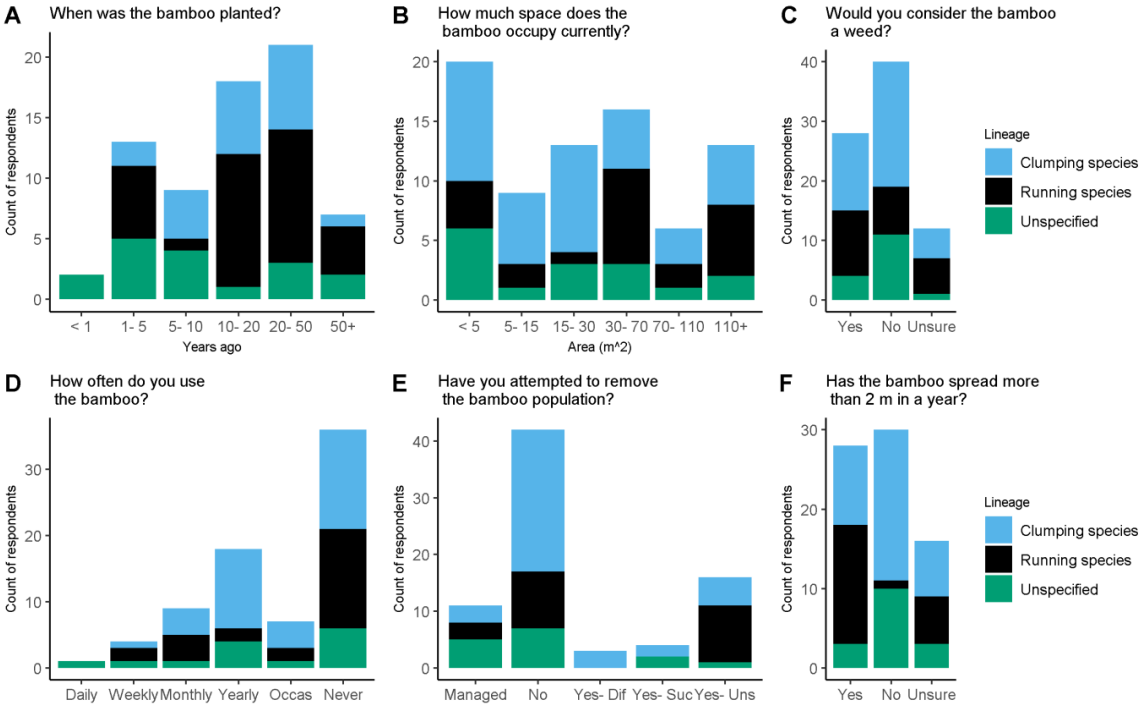

Figure 5.3. Respondent answers for six questions regarding the uses and perception of bamboos in South Africa. Answers are grouped by bamboo lineage/ type (clumping, running and unspecified species).

Most respondents were connected with the survey via Facebook (64%), followed by local email newsletters (14%), from an unspecified source (9%), word-of-mouth referrals (9%), or from their local conservancy (5%). This could have added bias to the pool of respondents, as only those with access to a computer and internet were included. However, we did achieve a good geographic coverage of participants - responses were received from across the country, although with an expected higher number of respondents from the major cities of Johannesburg, Durban and Cape Town (see **Figure S5.1**).

The historical literature was dominated by references to clumping tropical species from Asia, but only 49% (n=39) of questionnaire respondents had this type. Nearly a third 31% (n=25) of respondents reported having temperate running bamboo on their land, with the remaining 20% (n=16) being unspecified or comprising both types. This may give credence to the notion that there is preference for running species for ornamental horticulture. This is certainly true in the Northern Hemisphere where in Europe and the United States, perhaps due to the climatic similarity to Asia, running species native to temperate Asia have traditionally been preferred over tropical clumping species in the ornamental horticultural trade. For example, Kew Botanical Gardens, which was the epicentre for Victorian plant collections, has a bamboo

garden that still maintains a historical collection of almost entirely temperate species (*S. Canavan, pers. obs.*).

Given that temperate running species tend to be more invasive (Lieurance *et al.* 2018a), we expected that growth form would be an important factor explaining how respondents value or disvalue bamboo. We also expected that the pathways of introduction would differ for running and clumping species. This was true for three questions, where the type of bamboo (running, clumping or unspecified) was significantly associated with (1) the period when the bamboo was planted (X^2=22.01; df=10; p=0.015; **Figure 5.3a**); (2) whether respondents had attempted to remove or manage the bamboo (X^2=23.12; df=8, p<0.01; **Figure 5.3e**); and (3) whether the bamboo had spread more than 2 m in a year (X^2=17.83; df=8, p<0.01; **Figure 5.3f**). We interpreted these results to mean that: (1) the preference for planting clumping or running bamboos has changed over time; (2) landowners with clumping species were less likely to remove or manage the bamboo; (3) if control was attempted, it was more likely to have failed for running species; and, perhaps unsurprisingly; (4) respondents reported that the running species spread more often than clumping species, although there were reports of spreading clumping species.

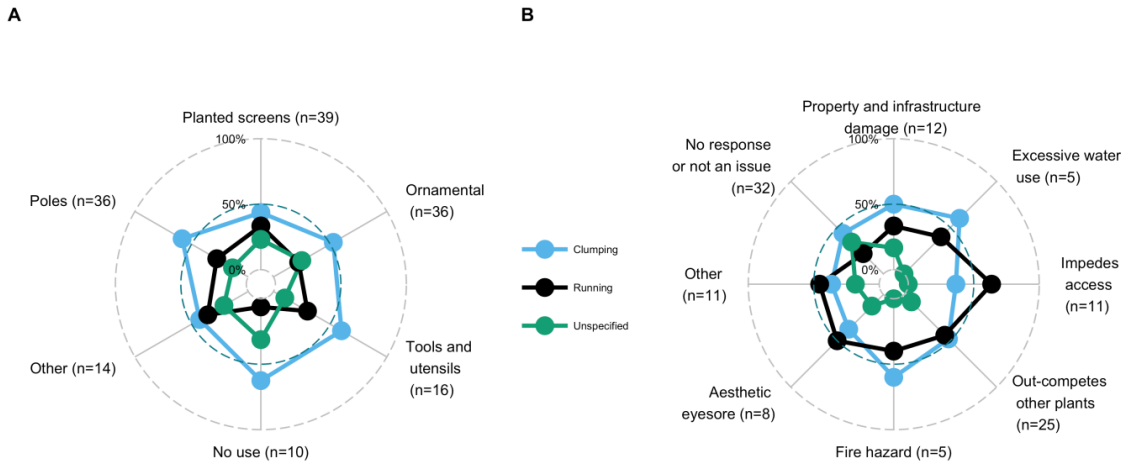

Figure 5.4. Respondents (n=77) were asked to list all the ways in which (A) they use bamboo; and (B) problems associated with invasive bamboo populations. Uses were classified into six categories and problems into eight categories. Respondents could answer multiple ways for how the bamboo is used or is problematic. The radar chart shows the proportion of respondents with running, clumping or unspecified species for each use or problem category e.g. for the 36 respondents who indicated that the bamboo is used for 'poles', 58% had clumping species, 28% had running species and 14% were unspecified.

The type of bamboo, however, did not influence (1) the size of the area that the bamboo occupied (**Figure 5.3b**); (2) whether respondents considered the bamboo a weed (Fig 3c); and (3) the frequency of use (**Figure 5.3d**). We would have expected running bamboos to be more likely considered weedy given their invasive nature, but this was not the case. A fairly high proportion of respondents (35%, n=28) did, however, consider bamboo (both running and clumping species) to be a weed in general. Whether respondents considered bamboo a weed was not related to the type of bamboo, but might be related to whether the bamboo is used by respondents. For example, 42% (n=32) of respondents answered that they never use the bamboo on their property; 50% (n=18) of these respondents viewed bamboo as a weed. Only 23% of the 24 respondents that use bamboo considered it to be a weed.

For many respondents, bamboo was a useful plant to some degree, but also a problematic one. Respondents were asked to score the usefulness of bamboo to them on a scale from 0 (no use) to 5 (very useful), and also how problematic they found the bamboo to be on a scale of 0 (no problems) to 5 (very problematic). The scores were not influenced by the type of bamboo for how useful and problematic responders found the bamboo to be is e.g. temperate bamboos are both liked and disliked, as are tropical species. When we compared the average score given for "usefulness" (m=2.28, s.d.=1.94) and "problematic" (m=2.22; s.d.= 1.94) there was no significant difference (W = 3172, p-value = 0.85; **Figure** 5.4) between the two groups. We take this to mean that respondents found bamboos both useful and problematic.

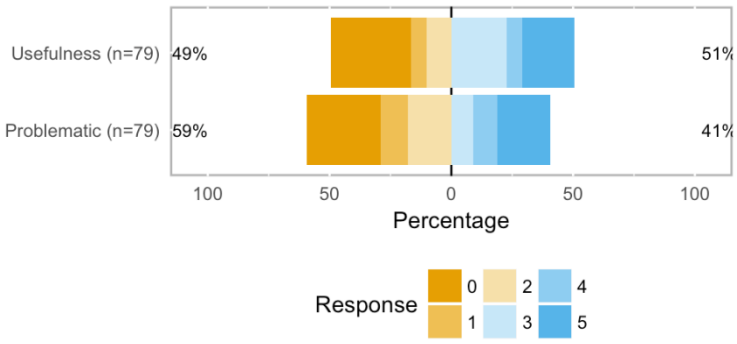

Figure 5.5. Respondents were asked to score the extent to which bamboos are useful (Is the bamboo a useful plant today?) and problematic (Does the bamboo cause any problems? e.g. excessive spreading,

difficult to control, fire hazard etc.), on a scale from 0 (no use/ no problem) to 5 (very useful/ very problematic). Colours and sizes in the bar plot indicate the percentage of respondents that answered for each level for usefulness and problematic. Being perceived having both uses and problematic at times indicates that bamboos may be a "conflict of interest" species in some instances.

When respondents were asked to list their uses of bamboo (predefined groups were provided for selection, and there was an option to add specific uses). We grouped the final answers into six categories (respondents could have given answers for multiple categories); planted screens (n=39; e.g. garden screens, wind breaks, perimeter plantings); ornamental purposes (n= 36); tools and utensils (n= 16 e.g. garden and kitchen tools, fishing rods); poles, (n=36 e.g. poles for constructions, trellises, fencing); no use (n=10); and other (n= 14 e.g. food, animal fodder, toys, wind chimes, leaf litter). The most commonly listed uses were for screens, poles and ornamental horticulture. Again, the type of bamboo did not influence how the bamboo was used (X^2=7.99; df=14; *p*=0.63). Temperate and tropical bamboos were used generally across the different groups (**Figure 5.3a**).

Similarly, when respondents listed the ways in which they find bamboo to be problematic, the type of bamboo did not influence the type of problem (X^2=16.73; df=14; *p*=0.27) (**Figure 5.4b**). We grouped the final answers into eight categories: no response/ no issue (n=32); out-competes other plants (n=25); property & infrastructure damage (n=12); impedes access (n=11); other reasons (n=11 e.g. labour intensive to maintain, emerging spikes (shoots) are dangerous to children, noisy in wind); aesthetic eyesore (n=8); and excessive water use (n=5). The most common issue that respondents reported in terms of negative impacts were that bamboo out-competes plants, causes damage to property and infrastructure, and requires excessive use of water. We did note that when respondents indicated that the bamboo impedes access a high proportion were running species (**Figure 5.3b**). Some respondents also remarked on the financial cost of managing the bamboo.

The questionnaire revealed that current perceptions towards bamboos vary widely, making bamboo a "conflict of interest group" – species are both valued and considered to be weeds. The mixed value placed on bamboo taxa may be explained by (1) the cultural integration during the long history of introduction and use, resulting in certain people now having a strong affinity with bamboos; and (2) the recent realization, and personal experience by landowners, that bamboos can have negative impacts, leading to negative perceptions among some groups. The difference in opinions may manifest itself more in places like South Africa due to the stark socio-economic contrasts that have existed and that still exist and which shape perceptions regarding plants in different contexts (Kull *et al.* 2011). For example, water usage by bamboos

may be important to rural farmers but less so for city-dwellers, whereas concerns relating to weediness of bamboos in tended gardens are of more concern to city-dwellers than farmers.

5.5 CONCLUSION

Bamboos have had a long history in South Africa where there have been multiple phases of introduction with multiple pathways and incentives for these events. Each phase has been closely aligned with socio-historical events in the region. The use of bamboo has historically not only benefited one group, but has been used by different demographic groups and across socioeconomic classes. It is clear that introductions have been driven by different groups e.g. Venda people and European settlers, which is perhaps unusual compared to other plant introductions. The story of bamboo in South Africa is thus an excellent example to explore (1) the initial motivations for introductions; (2) the process of cultural integration; and (3) the emergence of polarized attitudes as the species spread and become weedy over time have combined to create a complex tapestry of perceptions. Such perceptions must be considered when formulating national and regional strategies for sustainable environmental management.

6 Status report on alien bamboos in South Africa

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Contribution of authors: S.C., J.R.U.W., J.J.L.R and D.M.R. conceived the idea. S.C. carried out the field-work and genetic analysis. J.J.L.R. and S.K. advised on the genetic analysis. S.C. led the writing of the manuscript with inputs from all co-authors.

6.1 ABSTRACT

The increasing commercial cultivation of bamboos in South Africa has led to new introductions of various species into the country. The rate at which new species are being planted is a cause for concern regarding the potential for invasions. To understand the threats associated with new bamboo introductions we assess the outcomes of past introductions. To this end we review bamboos in South Africa to: (1) produce an inventory of introduced taxa; (2) assess the distribution of bamboos; and (3) determine the rate of spread of bamboo at a site where there is a high density of naturalised stands. We used a combination of expert opinion, literature, records of populations, and public participation to produce a species list and locate populations of alien bamboos in South Africa. As a second source of taxonomic information we also used DNA barcoding of leaf samples for two chloroplast gene regions (*rpl16* intron D4 and *trnG-trnT*). We found there to be ca. 26 species of bamboo recorded as introduced to South Africa. However, bamboos are an inherently complicated group to identify using both vegetative material and DNA barcoding techniques. For DNA barcoding, the *rpl16* intron could not differentiate species. The *trnG-trnT* region was found to be highly variable and our results suggest this region may hold promise as a DNA barcode for identification of bamboo species. We could not accurately identify all the species currently present in South Africa. However it was clear that the distribution of bamboos varied depending on the type of species (e.g. herbaceous, tropical or temperate) and the source of information (e.g. herbarium records, in-field observation or public contribution). Despite several instances of naturalisation, we did not find large invasive stands, nor any suggestions of widespread negative environmental impacts. However, caution should still be taken with regard to future introductions of bamboos for commercial cultivation as the species and nature of the plantings will most likely differ from the historical situation.

6.2 INTRODUCTION

There has been a major drive to promote the cultivation of bamboos in South Africa in the last decade for multiple reasons, especially as a feedstock for bioenergy and biofuels, for pulp and paper production, phytoremediation, and to provide general construction material (Scheba *et al.* 2017). Fast-growing and robust species from Asia are being promoted for these purposes (Buckingham *et al.* 2014, Scheba *et al.* 2017). Despite these economic incentives, there is concern that damaging invasions might occur in South Africa if widespread bamboo introductions and plantings take place, as is commonly observed for cultivated bamboos elsewhere in the world (Canavan *et al.* 2017b, Canavan *et al.* 2018b),

Concern has been expressed that alien grasses in general, including bamboos, have not been well studied in South Africa (Visser *et al.* 2017). However, with the development of the *National Environmental Management: Biodiversity Act* (NEM:BA, Act 10 of 2004) Alien & Invasive Species Regulations in 2014, more concerted efforts are being made to produce up-to-date inventories of alien taxa, including introduced grasses, present in South Africa. Milton (2004) published the first review of alien grasses in South Africa and produced a list of 114 taxa known to be present, including one species of bamboo (*Bambusa* sp.). In an updated assessment, Visser et al. (2016) listed an additional 143 alien grass species (a total of 256 species), including 17 species of bamboo. Visser et al. (2016) conclude that 11 of the 17 species of bamboos were probably introduced prior to the 1950s, some as early as 1866 (e.g. *Bambusa balcooa*). Even well-studied plants groups, e.g. Australian acacias (genus *Acacia*) in South Africa, can have surpringly outdated species lists (Magona *et al.* 2018). These issues highlight the need for better and continued monitoring, but also that new information sources should be explored to produce comprehensive and up-to-date inventories.

The burgeoning bamboo industry in South Africa, and evidence of problems with invasive bamboos in other parts of the world, calls for an assessment of past introductions as input to a comprehensive analysis of risks associated with bamboo cultivation. Despite South Africa's long history with bamboo introductions (Visser *et al.* 2017, Canavan *et al.* in review) there has never been a dedicated review to determine which species have been introduced, whether any species have become invasive, and what the current distribution of species is. No bamboo species are currently listed as invasive in South Africa, but this may be due to the relatively recent introduction (in the past few decades) of some taxa – it is well known that there is usually a lag of several decades between introductions and invasions (Rouget *et al.* 2016). To provide information required for a comprehensive assessment of the risks associated with the introductions bamboos and their cultivation in South Africa this paper sets out to: (1) compile an updated inventory of the alien bamboo species present in South Africa; (2) assess the distribution of bamboos in South Africa from historical records and field observations, and (3) determine the invasive status at a key site with a high density of bamboos.

6.3 METHODS

6.3.1 Compiling a list of introduced species and their distribution

Various sources were used to compile a list of alien bamboo taxa present in South Africa (**Figure 6.2**), including: (1) records from an online literature search (see Chapter 5); (2) herbarium records and data from the Southern African Plant Invaders Atlas (SAPIA; Henderson and Wilson (2017)), a regional comprehensive database on invasive alien plants; (3) the National Herbarium Computerized Information System (PRECIS online database http://newposa.sanbi.org/; Morris and Glen (1978)); (3) herbarium samples for South Africa listed on the Global Biodiversity Information Facility (GBIF 2016), an open access source of global biodiversity data. We removed duplicate data and filtered incomplete information. Synonyms were corrected using The Plant List (www.theplantlist.org accessed in March 2018).

Besides using herbaria records we undertook field sampling across South Africa (see **Figure 1a**) with the aim of identifying new species and populations that were not previously recorded. To locate populations we: (1) sought advice from local and regional conservation managers or experts working with invasive species; (2) compiled information from herbaria records (from the sources mentioned above); and (3) posted articles in local agricultural magazines appealing to the public for information on sites where bamboos were growing (**Figure 6.1a**; link to survey: https://goo.gl/forms/2V4kJLbcrM0CAvdr2). At each sampled site photographs were taken of the morphological features of the bamboo and of the site. Where possible, herbarium samples and fresh undamaged leafs were collected for genetic analysis (see below). All herbarium voucher specimens have been registered and deposited at the Stellenbosch University Herbarium (herbarium accession numbers pending). Samples were taken intermittently between 2014 and 2016.

6.3.2 Identification and DNA barcoding of species

DNA barcoding is an increasingly important component of biosecurity to identify alien species and is particularly useful for taxa that are not easily identifiable by their morphological characteristics (Armstrong and Ball 2005), as is the case with bamboos. The use of morphological characteristics in bamboo taxonomy is a challenge due to the infrequency of inflorescence and seed production in many woody species of bamboos (where normally identification is dependent on reproductive features).

To identify the species of our collected samples we used DNA barcodes of two different chloroplast regions. We used the primer set D4 which was developed specifically as a short, informative locus for

bamboos (Watts *et al.* 2008). The D4 set targets a highly variable *rpl16* intron chloroplast region. It has good, or better, resolution in bamboos than the commonly used *trnD-trnT* intergenic spacer (Watts et al. 2008). A second locus, the *trnG-trnT* region developed by S. Kelchner specifically for this study was also used. The *trnG-trnT* region has been found to be one of the most variable regions in the chloroplast genome for bamboos and currently considered to be the most promising locus for distinguishing bamboo species.

DNA extractions of collected leaf samples were performed using a modified version of the cetyltrimethylammonium bromide (CTAB) method as described by Doyle and Doyle (1990). Preserved and dried leaf tissue samples (~ 300 mg) were ground using a TissueLyser. 1 ml of CTAB extraction buffer was added to each sample and heated (65 °C) for 60 mins. To extract DNA, 200 µl of chloroform:isoamyl alcohol (24:1) was added (2 x), and precipitated using 600 µl of chilled isopropanol. DNA pellets were drained and washed using 1 ml of 70% ethanol. Samples were dried overnight and then re-suspended in 50 µl of MilliQ water. DNA concentrations were determined using a NanoDrop spectrometer (ND1000). The CTAB method gave a fairly high success rate (70%) for extracting DNA from our 40 test samples.

The *rpl16* intron ws amplified using the primers R1516 and sak16F with the following polymerase chain reaction (PCR) conditions: Initial denaturation at 80 °C for 5 min, followed by 35 cycles of denaturation at 95°C for 1 min, annealing (1 min ramp of 0.3 °C/s starting at 50 °C), and extension (1.5 min at 65 °C), and a final extension (4 min at 65 °C). The *trnG-trnT* region was amplified using the primers sak 71F and sak 72R with the following PCR conditions: Initial denaturation at 95 °C for 5 min, followed by 35 cycles of denaturation at 95°C for 1 min, annealing (1 min ramp of 0.3 °C/s starting at 48 °C – 60 °C), and extension (1.5 min at 72 °C), and a final extension (10 min at 72 °C).

Each 30 µl reaction contained ca. 300 ng of genomic DNA, 200 µM of each dNTP (Thermo Scientific, supplied by Inqaba Biotec, Pretoria, South Africa), 3 pmoles of each primer, 1 U Taq DNA polymerase (supplied by Seperation Scientific SA), 1X PCR reaction buffer and 2 mM $MgCl_2$.

PCR products were run on a 1% agar gel and visualised under UV light. Amplified DNA fragments were purified using the QIAquick PCR Purification kit (Qiagen, supplied by Whitehead Scientific, Cape Town, South Africa), and sequenced using the ABI PRISM BigDye Terminator Cycle Sequencing Ready Reaction kit (forward only) and an automated ABI PRISM 377XL DNA sequencer (PE Applied Biosystems, Foster City, CA, USA) and the forward primer used for PCR amplifcation.

To determine the taxoxonomic resolution of both DNA regions, we did BLAST searches of four test samples that represented four species from three genera (from both temperate and tropical bamboo lineages) for which we knew the species identity. We then compared the DNA sequence similarity to

the GenBank sequences to see whether they had a high sequence similarity (≥ 99%). This was done for both regions to see whether either method could be used to later match DNA sequencing data from unknown samples to reference samples in Genbank (See **Table S6.1**).

6.3.3 Assessing invasion rates of bamboos along the Nonoti River

During field sampling we observed many populations of bamboos along from the Nonoti river in KwaZulu-Natal, from its estuary inland (**Figure 6.3**). The surrounding area is a productive sugarcane growing region (Platford 1988). It is a unique site for having such a high bamboo density, most likely originating from historic plantings by sugarcane farmers for windbreaks and erosion control (see Chapter 5). The site provided a good opportunity to evaluate the changing distribution of bamboos over time. Further, the river itself is small but leads to the Nonoti estuary, one of eight estuaries of the KwaDakuza river systems, and supports a diversity of flora and fauna. If bamboos are spreading this could threaten the functioning and diversity of this ecosystem.

To assess the population expansion rate of the bamboos, we analysed temporal satellite images on Google Earth in 2006 and then in 2017. Tropical bamboos in this area are easily distinguishable from other background vegetation due to their large size, different colouration and more rounded shape. We were therefore able to identify and draw polygons around clumps or grouped clumps (n=96). We measured all clumps that were within 160 m on both sides of the Nonoti River. We pinned bamboos from the base of the estuary until populations became sparse (less than 1 observation per kilometre along the river way). The last bamboo clump measured was roughly 10 km inland from the coast, where the Gunqu river joins the Nonoti river (-29.257242, 31.307501). We used Google Maps street view to confirm that some mapped populations were indeed bamboos. We also referenced images of known sampled sites with new found ones on Google Earth to see whether they matched. We used the website Earth Point (www.earthpoint.com) to calculate the area of all measured polygons. The total area occupied by bamboos is a conservative estimate, as we probably missed some small populations and some occurring under dense tree cover. Although manually delineating bamboo populations using the polygon tool provides crude estimates, the levels of error are likely to be the same for the two sets of images.

Data for both 2006 and 2017 images were not normally distributed according to a Shapiro-Wilk normality test ($W=0.15521$, $p<0.001$). We therefore used a paired Wilcoxon Signed-Rank Test to test whether there was a significant difference in the areas of the different populations in 2006 compared to 2017. All analyses and data visuals were done in R 3.4.3 (R Core Team 2015).

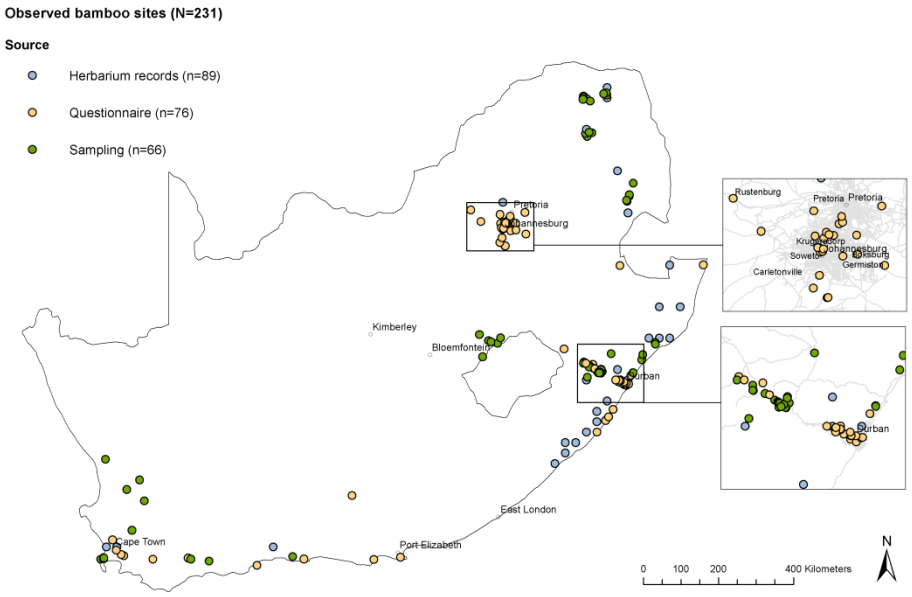
6.4 RESULTS

6.4.1 Introduction and presence of bamboo

The search of literature and herbarium records revealed 26 species of bamboos that are known to have been introduced to South Africa (**Table 6.1**). The actual number of alien bamboos in the country is however probably higher given the recent upsurge in importation of species for experimentation by private growers although many of these have not been documented or declared (*S. Canavan, pers. obs.*).

Bamboos are currently scattered across the country, with the exception of the Northern Cape, where there were no records, and Eastern Cape, where there were few records (**Figure** 6.1). We recorded 66 sites across South Africa with alien bamboo populations. Some sites were sampled multiple times as there were more than one species or the site was revisited. A majority (56%) of sites were found via suggestions from public and experts who responded to postings about the project on social media, magazines and email chains; specifically, 16 sites were suggested by local and regional conservation managers or experts working with invasive species and 19 sites were from the general public. 35% (n=23) of sites were happened upon by chance during sampling trips and 8 sites were found from herbarium records. One site was excluded as the species found there was determined to be the native species *Bergbambos tesselata.*

(A)



(B)

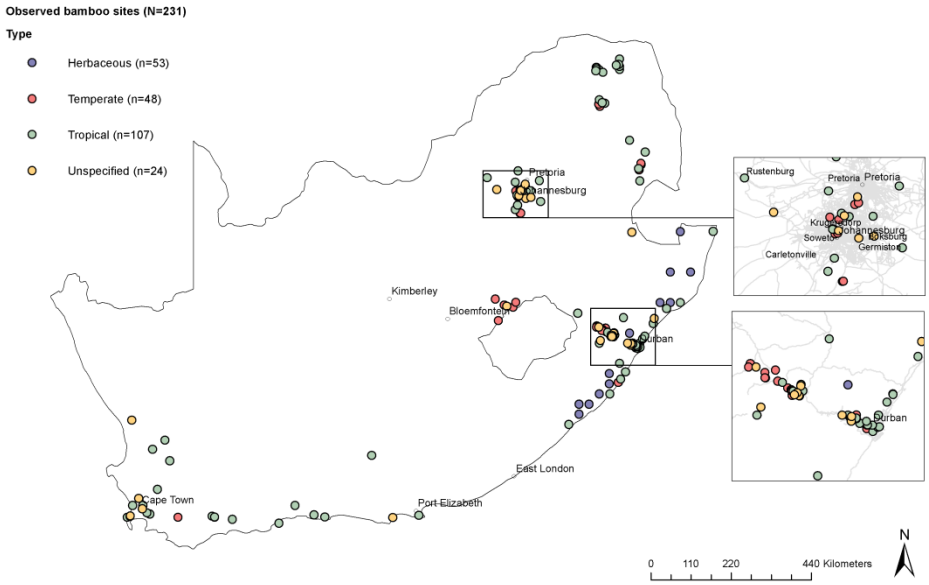


Figure 6.1 Observed populations of alien bamboo species in South Africa from 1896-2017 displayed according to (A) the data source (herbarium records, personal observations, and responses from an online questionnaire in 2017) and (B) the type of bamboo (herbaceous, temperate, tropical, and unspecified) from the source.

Almost half (48%; n=32) of sites were on a private land such as a smallholding, farm or business premises; 47% (n=31) were on public land such as road verges, waterways or government-owned sites including nature reserves and forestry plantations. Another three sites were established commercial bamboo plantations. More than half of the sites (54%; n=36) had populations that had escaped

cultivation (found beyond the property perimeter of the original planting site) or appeared to be naturalised in that they had self-sustaining populations beyond cultivation. The remaining populations were in gardens or farms and appeared to be planted and cultivated (46%; n=31). When we grouped the sampled population by lineage (as designated by Kellogg (2015)), half of the populations comprised tropical species (49%; n=33), 39% were temperate (n=26), one site had a herbaceous bamboo, and the remaining sites had multiple populations (n=3) or the type was unknown (n=4). Responses from the online questionnaire, as well as from our sampling efforts, indicated the prevalence of temperate species in urban areas, but herbarium observations only indicated the presences of tropical and herbaceous species.

Bamboos were found at low altitudes from 33 m to 1700 m above sea level. However, temperate bamboos tended to be at higher altitudes on average (1231 m) compared to tropical species (583 m; see **Figure S6.1**). No populations were observed to be flowering or seeding. Although some landowners mentioned that they had seen flowering (in what is suspected to be *Bambusa balcooa*), we were unable to confirm this. Most populations were close to a water source.

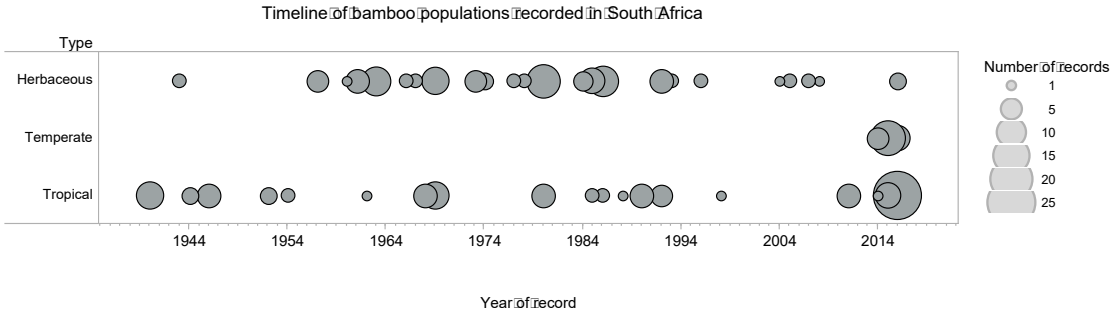


Figure 6.2 Populations of bamboo sampled in South Africa in the past 70 years separated by growth form of species. Information comes from a combination of herbaria records and observations made during the timeline of this study (grey shaded area).

6.4.2 Identification of species

We were unable to reliably identify our samples to the species level with the absence of a regional expert that specialises in bamboo taxonomy and as our specimens lacked reproductive structures. We were, however, able to group populations by the type of bamboo (temperate, tropical or herbaceous). The type of bamboo is related to the growth form, with temperate species having a running form with woody culms, and tropical also having woody culms but grow in a clumping manner; herbaceous species are smaller and more grass-like. Running temperate species spread rapidly compared to clumping tropical species, and therefore separating bamboos by growth form is an important distinction for predicting invasion potential (Lieurance *et al.* 2018b).

We were able to successfully sequence both the *rpl116* and *trnG-trnT* regions. However, we were unable to correctly assign a taxonomic rank based on the BLAST results of our test samples. For example, the *rpl116* region retrieved a perfect match rate (100%) with multiple species from different genera and even different lineages (see **Table S6.1**). This shows that there is low resolution between species for this DNA region and that this approach is not appropriate for identifying bamboos to the species, or even genus, level. The *trnG-trnT* region was much more variable. However, with the developed primers we were only able to sequence ca. 800 bp in one direction (despite the amplicon length being much longer), therefore, we were unable to reliably compare to accessions available in Genbank.

6.4.3 Nonoti River site

There was a significant increase in the overall average area of measured clumps from 2006 to 2011 ($V=1524$, $p<0.01$), although the rate of expansion was slow. In 2006, bamboo populations occupied an estimated area of 175,456 m^2. In 2017, there was a 6% increase in area (total area 186,454 m^2). The bamboo clumps increased in size at a rate of 2.52 m over 11 years or < 0.3 m a year, on average. However, not all sites showed an increase in size; of the 95 clumps, 61% (58 clumps) had increased, with the remaining 37 clumps reducing in size (mostly only marginally). We did not identify clear spreading of populations, but rather that clumps had increased or bulked in size over the 5-year period. We found only one new population (-29.297996, 31.387759) that were present in 2017, but not in 2006.

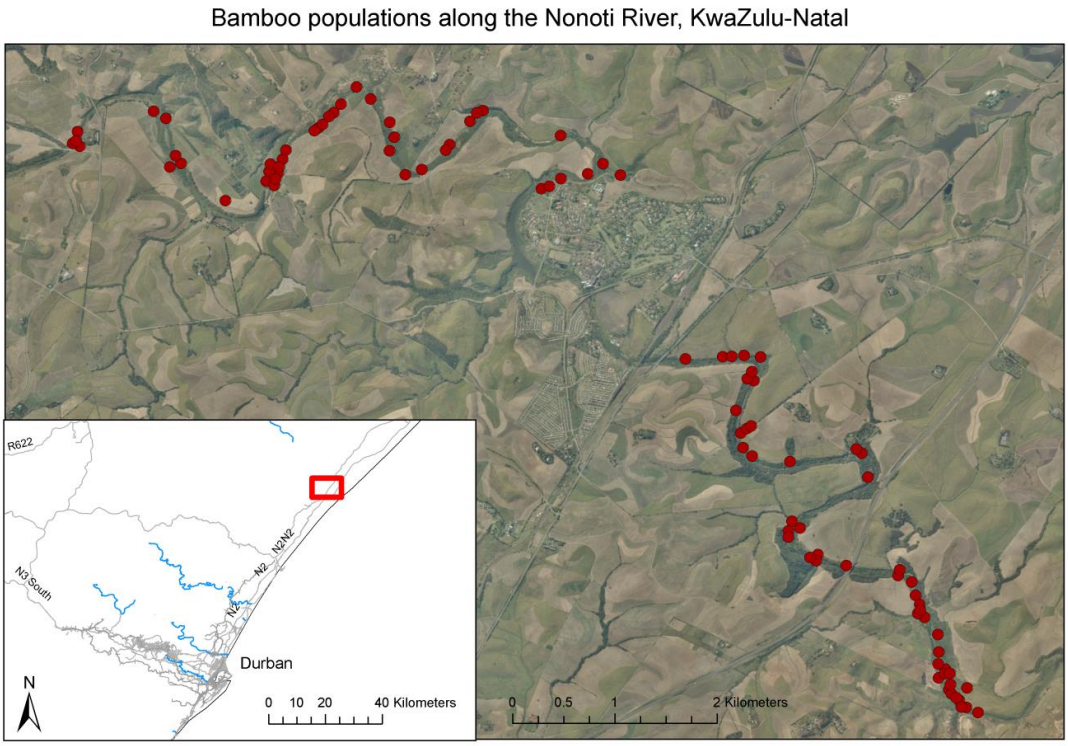


Figure 6.3 *Bambusa* populations (red circles) along the Nonoti river.

6.5 DISCUSSION

In this study, it was clear that bamboos are an inherently difficult group to identify accurately and we have not yet obtained accurate identification tools to differentiate the species that are present in South Africa. Secondly, we determined that there has been an under-reporting of the presence of bamboos around the country, particularly of the more invasive temperate species found in urban areas. And lastly, we identified that the threat of certain species is not adequately reflected in current legislation.

6.5.1 Issues in identification of species

This study confirmed that bamboos are an inherently complicated plant group to accurately identify. We also found that identification of bamboos via DNA barcoding was not possible in this study due to the low resolution between species using the *rpl116* chloroplast region. However, the *trnG-trnT* region was highly variable between species in our test samples which was also confirmed in another study that mapped the entire genome of six woody bamboos (Zhang *et al.* 2011). We suggest that future work should focus on the development of internal primers to lengthen the *trnG-trnT* region as this will likely provide a promising area for

differentiating species. However, one should be cautious, even if if this region is informative and reference data is avialble on GenBank, as a reliable inference would hinge upon the correct identification of reference material deposited into Genbank. For example, more than a third (36.2%) of bamboo samples sequenced and uploaded to GenBank (N=366 species) are synonyms, indicating an inherent issue with perhaps poor taxonomy of listed species, as well as a lack of resolution between known genetic markers.

The identification issues associated with bamboos are a general problem in invasion science, in that taxonomical-related errors are common in ecological datasets (McGeoch *et al.* 2012, Murray *et al.* 2017, Magona *et al.* 2018). For example, a recent study by Zermoglio *et al.* (2016) found that only 47% of 1000 scientific names of vertebrates listed in digitized biocollections were correctly validated. Such errors in alien species identification and their subsequent listing is a serious issue for biosecurity and risk assessments. Even if targeted species are known to be high risk, the ability to correctly identify them visually or through DNA barcoding is currently limited.

Table 6.1 The introduction and current presence of alien bamboos in South Africa as determined by herbarium and literature records. Synonyms have been corrected according to The Plant List (www.theplantlist.org) in March 2018.

Species	Herbarium record	Literature record of presence	Current status	Provinces recorded
Olyra latifolia L.	Yes	Yes	Not known	KwaZulu-Natal
Himalayacalamus hookerianus (Munro) Stapleton	No	Yes	Not known	Not known
Phyllostachys aurea Rivière & C.Rivière	No	Yes	Not known	Not known
Phyllostachys nigra (Lodd. ex Lindl.) Munro	No	Yes	Not known	Not known
*Phyllostachys viridiglaucescens (*Carrière) Rivière & C.Rivière	No	Yes	Not known	Not known
Pleioblastus fortunei (Van Houtte) Nakai	No	Yes	Not known	Not known
Pleioblastus simonii (Carrière) Nakai	No	Yes	Not known	Not known
Pseudosasa hindsii (Munro) Nakai	No	Yes	Not known	Not known
Bambusa balcooa Roxb.	Yes	Yes	Naturalised	Gauteng, Limpopo, Mpumalanga, KwaZulu-Natal, Western Cape
Bambusa bambos (L.) Voss	Yes	Yes	Cultivated	KwaZulu-Natal
Bambusa flexuosa Munro	No	Yes	Not known	Not known
Bambusa multiplex (Lour.) Raeusch. ex Schult	No	Yes	Naturalised	Western Cape
Bambusa oldhamii Munro	No	Yes	Not known	Not known
Bambusa polymorpha Munro	Yes	Yes	Not known	KwaZulu-Natal
Bambusa textilis McClure	No	Yes	Not known	Not known
Bambusa vulgaris Schrad.	Yes	Yes	Naturalised	KwaZulu-Natal, Western Cape
Dendrocalamus asper (Schult.) Backer	No	Yes	Not known	Not known
Dendrocalamus giganteus Munro	No	Yes	Not known	Not known
Dendrocalamus latiflorus Munro	No	Yes	Not known	Not known
Dendrocalamus membranaceus Munro	No	Yes	Not known	Not known
Dendrocalamus strictus (Roxb.) Nees	Yes	Yes	Not known	Limpopo, Mpumalanga, KwaZulu-Natal
*Drepanostachyum falcatum (*Nees) Keng f.	No	Yes	Not known	Not known
*Melocanna baccifera (*Roxb.) Kurz	No	Yes	Not known	Not known
*Ochlandra scriptoria (*Dennst.) C.E.C.Fisch	No	Yes	Not known	Not known
Oxytenanthera abyssinica (A.Rich.) Munro	No	Yes	Not known	Not known
Schizostachyum dullooa (Gamble) R.B.Majumdar	No	Yes	Not known	Not known
Thyrsostachys siamensis Gamble	No	Yes	Not known	Not known

6.5.2 Distribution

We found that the distribution pattern of bamboo is, perhaps unsurprisingly, influenced by the type of bamboo. This was particularly true for the herbaceous bamboo, *O. latifolia*, which is restricted to coastal forests from the Eastern Cape up to Mozambique (**Figure** 6.1**b**). Temperate bamboos are associated with urban areas or areas with high human population densities most likely due to it being commonly used as a garden ornamental. Tropical bamboos have a more varied distribution and are found across the country, naturalised in rural areas as well as growing in gardens (**Figure S6.1**). The areas where tropical bamboos grew also covered a greater variation in environmental conditions. The wide distribution of tropical bamboo might be influenced, in part, by the long introduction history of these species, and multiple introduction events by different groups of people (Chapter 5, Canavan et al. in review). Unsurprisingly, bamboos were not found where there is low rainfall and extreme temperatures.

We also found that the distribution and type of species reported were different, depending on the source of information. The observations from this study suggest that there is a growing popularity for temperate species in gardens which has gone undetected in national alien species databases. Given that temperate species pose a greater invasion risk (Lieurance *et al.* 2018b), there could be a lag between temperate species being planted in gardens and them naturalising in surrounding areas. Of the 25 temperate populations observed during sampling, 48% (n=12) were found to be spreading beyond their planted site (e.g. under perimeter walls), and/ or there were clear attempts made to manage the bamboo via manual clearing or burning. In a cultivated setting temperate species are aggressive in their growth, and should be carefully monitored so that they do not become naturalised in areas where they cannot be managed.

Overall, we found combining both expert and public observations was useful. This was possible as woody bamboos are large in size as well as being quite distinctive to other native vegetation in South Africa, making them an easy group for public sightings. However, as for many other grasses, especially smaller species that are more discreet, invasions are often not noticed and/or reported (Visser *et al.* 2017).

6.5.3 Evidence of increase in area, but not much spread

At the Nonoti site, we did not find clear evidence that the bamboo populations were invasive in that they were spreading rapidly (i.e. more than 2 m a year; Richardson *et al.* (2011)). However, we did find that the clumps had increased in size. There are a number of possible reasons why

the bamboo has not spread: (1) the surrounding area is under cultivation and is highly managed, and therefore the ability of bamboo populations to move beyond the river banks to the adjacent landscape is limited (although there was no evidence of the bamboos being directly targeted for clearing); (2) the populations are water dependant and cannot spread far from the river; and (3) there is a lag phase in the bamboo populations spreading—substantial spread might only occur through seed dispersal (no flowering has been observed to date). In general, bamboo populations are long-lived and spread vegetatively, and so spread and impact might take decades (Crooks 2005).

Despite a lack of substantial spread, the bamboos might be having negative impacts on the river ecosystem [cf. naturalised *Bambusa* species along rivers in Central America (Blundell *et al.* 2003)]. More in-field research would be needed to understand the effects of the populations on the ecology as well as hydrology of the river system. It would also be worth further investigation to determine if the presence of all clumps were directly planted or have new populations been established further down the river from initial planting sites. Either way, given that the populations have potential for impacts in the river system, targeted programmes to manage and remove populations would likely have high success rate due to the slow spread rates of the population.

6.5.4 Listing of invasive bamboos in legislations

In South Africa, currently only two bamboo taxa are listed under the most recent 2016 NEM:BA A&IS Regulatory Lists: *Sasa ramosa* (Makino) Makino & Shibata and the genus *Arundinaria* Michx – both in category 3 (which means that propagation and selling is prohibited). *Sasa ramosa* is a small temperate woody bamboo native to Japan. We found no evidence of *S. ramosa* being invasive in South Africa, or elsewhere (Canavan *et al.* 2017b). The reason for listing of this species and of the genus *Arundinaria* is unclear. The genus *Arundinaria* includes three ‘cane’ species that are native to North America. None of these species are widely introduced or are known to be invasive (Canavan *et al*. 2017). The listing of this genus may be due to the confusing taxonomic history of the group which was only stabilized in 2009. *Arundinaria* was initially a large genus that encompassed important woody species from Asia that have now been reassigned to other genera including *Pleioblastus*, *Pseudosasa*, *Guadua* and *Fargesia*. The listing of the genus was likely intended to target Asian temperate species of *Pleioblastus* and *Pseudosasa* which are known to be invasive. The taxonomic confusion of the group has been reflected in current regulations, and therefore future listing of bamboo species needs to be updated to better reflect; (1) current taxonomic

designations; and (2) the invasion risks posed.

6.5.5 Management recommendations

In summary, we found no evidence of major bamboo invasions in South Africa. While this suggests that the risk of invasions and impacts is low, there processes should be established to assess individual species, as many of the horticultural species are only recent introductions that could still have substantial negative impacts. Caution should also be taken with regard to future introductions of bamboos for commercial cultivation as the species and nature of the plantings will most likely differ from the historical situation. Finally, substantial negative impacts might also occur if bamboos are given opportunities to invade forest ecosystems, or if large stands of bamboos were to flower (Lalnunmawia *et al.* 2005, Pagad 2016).

7 General discussion

This dissertation used a combination of desktop reviews, field-based sampling of populations, a questionnaire involving public participation, and genetic analyses to produce an integrated understanding of how human-usage has aided in the introduction and has affected the invasion status of bamboos (and other tall-statured grasses). I show that bamboos have been a popular taxonomic group for dissemination around the world due to traits conferring socioeconomic desirability. Many bamboos are synanthropic species, in that they have benefited from human activity or the habitats that humans create around them. The results of the dissertation confirm how the invasion process for cultivated plants is closely aligned with human activities through answering the following questions (See **Table 7.1** for a summary of key findings):

1. What were the outcomes of past biogeographic experiments distributing bamboos?
2. Which species have been selected for introduction?
3. Do some bamboos have inherently more invasive traits over others?
4. Do those bamboos that have become invasive simply have traits that make them more desirable to humans which has increased the likelihood of their widespread introduction?

Table 7.1. Key findings from dissertation involving human usage and plant invasions from each chapter.

Key findings	**Example from dissertation**
1. Plant invasions often stem from socioeconomic factors rather than ecological ones	Human selection and socio-historical events have directly determined which bamboos have been distributed and become invasive.
2. Features of taxa that are valuable to humans increase the likelihood of introduction	Large woody bamboos have been cultivated and introduced more often than other types of bamboos.
3. The activity and the usage in the native range by humans influence a species to be introduced	In Asia, native bamboos have had a deep-rooted history, and these are the species that have been extensively introduced and used worldwide, despite the large number of species native to other regions.
4. The more a species is cultivated the higher rate it is introduced	The number of cultivars a bamboo has is associated with the number of regions to which it has been introduced
5. The more a species has been intentionally introduced there is a greater body of literature and interest online associated with it	Bamboo species that have been widely introduced have more online literature associated with them.

6.	**Activity and disturbances of a habitat can influence the weedy potential of native species**	Human disturbances (i.e. logging) provide opportunities for certain bamboos to become over dominant in forests in their native range.
7.	**Certain taxa have generalizable characteristics that influence their selection by humans and the recent pathways of introductions**	Tall-statured grasses are selected for biofuel, phytoremediation and other environmental uses because of their fast-growth rates, biomass production, and other traits.

In the global review of the movement of bamboos (Chapter 2), I produced an extensive inventory of bamboo species, and documented where they are globally distributed both in their native and introduced range. In consolidating records from multiple sources, I found that there were considerably more species alien to regions than previously thought. This is in line with a recent study by Seebens *et al.* (2017) which found that a quarter of 16,019 records of alien plant species had not been recorded as aliens prior to 2000. The increased number of alien bamboos reported may simply reflect that previous inventories did not detect or adequately record introductions. There has also most likely been an emergence of new introductions in line with a global increase in trade and movement of alien species. Overall, it is clear that humans have profoundly influenced the distribution patterns of bamboos.

Like other global reviews of the introduction history of diverse plant groups (Pyšek *et al.* 2008, Richardson and Rejmánek 2011, Moodley *et al.* 2013, Novoa *et al.* 2015), I found that the dissemination of alien bamboos has not been random. The selection criteria for which bamboos have been distributed can, in part, be explained by the following factors: (1) how useful a species is (i.e. is it more likely to be collected and disseminated if it has clear uses?); (2) historical events (e.g. the extensive trade-routes from Asia to other European colony outposts); and (3) activities in the native range (i.e. is the plant used and cultivated?). These factors influencing introduction efforts are not unique to bamboos, but they are particularly important in bamboos which require intensive cultivation efforts to establish populations in new locations (unintentional introductions are infrequent, if they ever occur).

In particular, we found that there has been a clear preference for the introduction of large Asiatic species and those that have a greater number of cultivars – indicating that higher utility increases the likelihood of introduction and dissemination. Despite the high diversity of native bamboos in South America, there have been few introductions of species from this region around the world. Cultivar diversity, or direct selective breeding by humans, indicates that activities of cultivation in the native range influence the probability of intentional distribution.

Furthermore, it supports the notion that propagule pressure is a universally important factor in facilitating invasions (Colautti et al. 2006).

We also identified that other activities in the native range, such as logging and intentional range expansion by humans, have been major drivers of the spread and have increased the abundance of populations in native forests (as seen in the global impact review in Chapter 3). Specifically, the facilitated dominance of many native bamboos in forests has been enhanced by human activities associated with increased disturbance which has led to major environmental impacts. Most notable in this regard has been the reduction of tree recruitment rates in both temperate and tropical forests. This finding has important implications for forest conservation, as managers must also consider how human activity has altered the composition and abundance of native species.

The impacts are a result of certain competitive features generally seen across woody species of bamboo, namely the high production of biomass, fast growth rates, and supporting rhizome networks. These features, however, are also not unique to bamboos, and other tall grass species can alter communities in a similar fashion. Further, tall grasses have similar pathways of introduction e.g. for biofuels, phytoremediation and soil stabilisation. In Chapter 4 this generalisation was extended to other grasses. We classified the group based on these impacts as a functional group which we termed “tall-statured grasses”. We found that tall stature (plant height) is an important trait for naturalisation success globally. However, we found that bamboos should be analysed separately from other grasses in terms of naturalisation rates. Overall, the impacts of the functional group of tall-statured grasses, including bamboos, is useful for producing generalised management plans and making predictions for future introductions of high-risk species.

Chapters 5 and 6 focused on the introduction of bamboos to South Africa as a case study. This country has had a turbulent history with the intentional introduction of invasive alien species, although research has largely focused on tree invasions resulting from introductions for forestry, sand stabilization and other purposes. When we explored the socio-historic narrative around bamboo introductions, we found the story to be a unique and fascinating one, that differs from other taxonomic groups, for a number of reasons: (1) there have been multiple surges of introductions that have been driven for different reasons and by different groups of people; (2) bamboos have been used by different social classes and demographic groups over time; and (3) there is evidence that bamboos have become entwined with the cultures of certain groups of

people. There is a complex tapestry of perceptions towards bamboo; they can be classified as a 'conflict of interest' group, as different groups of people value and dislike bamboos.

The last chapter assessed which species are present in South Africa and where they are distributed, to help guide future management objectives. At one site along the Nonoti River, where bamboos are dense, we assessed whether populations were invasive. Surprisingly, we found no evidence that the bamboos were spreading, possibly indicating a lag phase. Further work is needed to determine what proportion of the populations along the Nonoti River are the result of intentional plantings as opposed to escapes from initial planting sites. Regardless of whether invasions are occurring or the populations are the result of planting, the density and dominance of bamboos along the river are likely having impacts. Future work should quantify such impacts.

The last chapter also attempted to identify sampled populations through morphological and through DNA barcoding. However, we found the identification of the group to be particularly challenging. It is clear that even expert opinion and barcoding techniques cannot accurately identify species. There needs to be better acknowledgment that certain groups such as bamboos are very difficult to identify to the species level. On the other hand, we found for tall-grasses (in Chapter 4) that there are invasive taxa below the species level such as invasive genotypes within species as well as invasive cultivars. This presents challenges on how to regulate invasive taxa beyond the species level.

In summary, this dissertation has shown that in the case of bamboos, human usage is the main factor explaining how taxa progress along the introduction-naturalisation-invasion continuum. Bamboo spread relies on both human-mediated distribution of propagules and human-induced environmental changes that are advantageous to certain species (both in their native and introduced ranges).

Future introductions of bamboos and tall-statured grasses will most likely differ from the historical situation, not just in South Africa, but around the world due to the global movement promoting biofuels and other wonder plants for environmental mediation purposes. Specifically, traits selected for the purpose of bioenergy production (e.g. fast growth rates) will influence future selection and cultivation of species. It is possible in some regions there will be a degree of cultural integration surrounding bamboo as people become accustomed to bamboo-planted landscapes or bamboo-based products. However, whether the current perceptions of bamboo

will continue is unlikely if impacts continue to occur and are realised. Furthermore, impacts of bamboos in both the native and introduced ranges will most likely continue and even intensify, if not managed due to the increasing disturbance of forests globally.

Studying bamboos has provided further insights into the role of humans in shaping new biotas. Specifically, I have shown how with intentional introductions there is a clear 'human filter' that is relevant to all stages of the invasion process. If a species has a desirable trait, this will influence its probability of being selected and cultivated, but will also influence the types of impacts that can be expected in receiving ecosystems. However, selected traits vary depending on the reason for introduction (e.g. economic use, human enjoyment, and environmental problems). And further, the motivation for the introduction of certain taxa is not static but fluctuates with which taxa are fashionable, desirable or conveniently accessed at different times.

The results of this dissertation have value for the field of invasion science in general – exploring correlates of introduction and invasion are most likely applicable to other taxonomic groups. Identifying socio-economic drivers of intentional introduction help in making projections of how the composition of flora and fauna will be altered in the future. Such information can also contribute to efforts in preventing or reducing the selection of particularly weedy species (such as those known to cause impacts in the native range). Further work looking at generalisations beyond grasses and plants, could provide additional insights into the role of humans in facilitating biological invasions.

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Appendices

Table S2.1. List of Bambusoideae species (1662 species) based on accepted taxa from Kew's GrassBase (http://www.kew.org/data/grasses-syn.html) updated to include recent literature on new species and other changes in classification that have been published up until September 2015, described at the generic level in Kellogg (2015). Updates were contributed by bamboo taxonomy specialist Lynn G. Clark (Iowa State University) and grass taxonomy specialist, Maria S. Vorontsova. *232 species have been introduced outside of their native range (numbers following species indicate the number of introduced regions), †12 species are referenced as being invasive [?]11 species have unknown or disputed native ranges. Note that the list does not include contemporary hybrids.

Acidosasa breviclavata
Acidosasa brilletii
Acidosasa carinata
Acidosasa chienouensis
Acidosasa chinensis
Acidosasa edulis
Acidosasa guangxiensis
Acidosasa lingchuanensis
Acidosasa nanunica
Acidosasa notata
Acidosasa purpurea
Acidosasa venusta
Actinocladum verticillatum
Agnesia lancifolia
Alvimia auriculata
Alvimia gracilis
Alvimia lancifolia
Ampelocalamus actinotrichus
Ampelocalamus breviligulatus
Ampelocalamus calcareus
Ampelocalamus hirsutissimus
Ampelocalamus luodianensis
Ampelocalamus melicoideus
Ampelocalamus mianningensis
Ampelocalamus microphyllus
Ampelocalamus naibunensis
Ampelocalamus patellaris
Ampelocalamus saxatilis
Ampelocalamus scandens
Ampelocalamus yongshanensis
Annamocalamus kontumensis
Apoclada simplex
Arberella bahiensis
Arberella costaricensis
Arberella dressleri
Arberella flaccida
Arberella grayumii
Arberella lancifolia
Arberella venezuelae
Arthrostylidium angustifolium
Arthrostylidium auriculatum
Arthrostylidium banaoense
Arthrostylidium berryi
Arthrostylidium canaliculatum
Arthrostylidium chiribiquetense
Arthrostylidium cubense
Arthrostylidium distichum
Arthrostylidium ecuadorense
Arthrostylidium ekmanii
Arthrostylidium excelsum
Arthrostylidium farctum
Arthrostylidium fimbriatum
Arthrostylidium fimbrinodum
Arthrostylidium grandifolium
Arthrostylidium haitiense
Arthrostylidium judziewiczii
Arthrostylidium longiflorum
Arthrostylidium merostachyoides
Arthrostylidium multispicatum
Arthrostylidium obtusatum
Arthrostylidium pubescens
Arthrostylidium punctulatum
Arthrostylidium reflexum
Arthrostylidium sarmentosum(1)*
Arthrostylidium scandens
Arthrostylidium schomburgkii
Arthrostylidium simpliciusculum
Arthrostylidium urbanii
Arthrostylidium venezuelae
Arthrostylidium virolinense
Arthrostylidium youngianum
Arundinaria appalachiana(1)*
Arundinaria gigantea(6)*
Arundinaria tecta
Athroostachys capitata
Atractantha amazonica
Atractantha aureolanata
Atractantha cardinalis
Atractantha falcata
Atractantha radiata
Atractantha shepherdiana
Aulonemia amplissima
Aulonemia aristulata
Aulonemia bogotensis
Aulonemia boliviana
Aulonemia bromoides
Aulonemia chimantaensis
Aulonemia cincta
Aulonemia cochabambensis
Aulonemia david-smithii
Aulonemia deflexa
Aulonemia dinirensis
Aulonemia effusa
Aulonemia fuentesii
Aulonemia glaziovii
Aulonemia goyazensis
Aulonemia haenkei
Aulonemia herzogiana
Aulonemia hirtula
Aulonemia humillima
Aulonemia insignis
Aulonemia jauaensis
Aulonemia laxa
Aulonemia longiaristata
Aulonemia longipedicellata
Aulonemia madidiensis
Aulonemia nitida
Aulonemia notata
Aulonemia parviflora
Aulonemia patriae
Aulonemia patula
Aulonemia prolifera
Aulonemia pumila
Aulonemia purpurata
Aulonemia queko
Aulonemia radiata
Aulonemia ramosissima
Aulonemia robusta
Aulonemia rubraligulata
Aulonemia scripta
Aulonemia setigera
Aulonemia setosa
Aulonemia soderstromii
Aulonemia subpectinata
Aulonemia tremula
Aulonemia trianae
Aulonemia verrucosa
Aulonemia viscosa
Aulonemia xerophylla
Aulonemia ximenae
Aulonemia yanachagensis
Bambusa affinis
Bambusa alamii
Bambusa albolineata
Bambusa alemtemshii
Bambusa amahussana
Bambusa amplexicaulis(1)*
Bambusa angustiaurita
Bambusa angustissima
Bambusa aristata
Bambusa arnhemica
Bambusa assamica
Bambusa aurinuda
Bambusa australis
Bambusa balcooa?(16)*
Bambusa bambos†(40)*
Bambusa barpatharica
Bambusa basihirsuta
Bambusa basihirsutoides
Bambusa beecheyana(6)*
Bambusa bicicatricata
Bambusa binghamii
Bambusa blumeana?(15)*
Bambusa boniopsis
Bambusa brevispicula
Bambusa brunneoaciculia
Bambusa burmanica
Bambusa cacharensis
Bambusa cerosissima
Bambusa chungii(1)*
Bambusa chunii
Bambusa clavata
Bambusa comillensis
Bambusa contracta
Bambusa copelandii
Bambusa corniculata
Bambusa cornigera
Bambusa crispiaurita
Bambusa dampaeana
Bambusa diaoluoshanensis
Bambusa dissimulator(4)*
Bambusa distegia
Bambusa dolichoclada(3)*
Bambusa duriuscula
Bambusa emeiensis(1)*
Bambusa eutuldoides(2)*
Bambusa farinacea
Bambusa fimbriligulata
Bambusa flexuosa(1)*
Bambusa fruticosa
Bambusa funghomii
Bambusa garuchokua
Bambusa gibba
Bambusa gibboides
Bambusa glabrovagina
Bambusa glaucophylla
Bambusa grandis
Bambusa griffithiana
Bambusa guangxiensis
Bambusa hainanensis
Bambusa heterostachya(1)*
Bambusa inaurita
Bambusa indigena
Bambusa insularis
Bambusa intermedia(1)*
Bambusa jacobsii
Bambusa khasiana
Bambusa kingiana(1)*
Bambusa kyathaungtu
Bambusa lako(2)*
Bambusa lapidea
Bambusa latideltata
Bambusa laxa
Bambusa lenta
Bambusa lineata
Bambusa longipalea
Bambusa longispiculata(13)*
Bambusa macrolemma
Bambusa macrotis
Bambusa maculata
Bambusa majumdarii
Bambusa malingensis(4)*
Bambusa manipureana
Bambusa marginata
Bambusa merrillii
Bambusa mitis
Bambusa mizorameana
Bambusa mohanramii
Bambusa mollis
Bambusa multiplex?(58)*

Bambusa mutabilis
Bambusa nagalandiana
Bambusa nairiana
Bambusa nepalensis
Bambusa nutans(3)*
Bambusa odashimae(1)*
Bambusa oldhamii(21)*
Bambusa oliveriana(2)*
Bambusa ooh
Bambusa pachinensis
Bambusa pallida
Bambusa papillata
Bambusa papillatoides
Bambusa pervariabilis(1)*
Bambusa pierreana
Bambusa piscatorum
Bambusa polymorpha(12)*
Bambusa procera
Bambusa prominens
Bambusa ramispinosa
Bambusa rangaensis
Bambusa rectocuneata
Bambusa remotiflora(1)*
Bambusa riauensis
Bambusa rigida
Bambusa riparia(1)*
Bambusa rongchengensis
Bambusa rugata
Bambusa rutila
Bambusa salarkhanii
Bambusa semitecta
Bambusa sesquiflora
Bambusa sinospinosa(1)*
Bambusa sinthana
Bambusa solomonensis
Bambusa stenoaurita
Bambusa subaequalis
Bambusa subtruncata
Bambusa surrecta
Bambusa teres
Bambusa textilis†(12)*
Bambusa thalawwa
Bambusa thorelii
Bambusa transvenula
Bambusa truncata
Bambusa tsangii
Bambusa tulda(14)*
Bambusa tuldoides(27)*
Bambusa utilis(1)*
Bambusa valida
Bambusa variostriata(1)*
Bambusa villosula
Bambusa vinhphuensis
Bambusa virginalis
Bambusa viridis(5)*
Bambusa vulgaris†?(127)*
Bambusa wenchouensis
Bambusa wiesneri
Bambusa xiashanensis
Bambusa xueana
Bashania fargesii
Bashania qingchengshanensis
Bergbambos tessellata(3)*
Bonia amplexicaulis
Bonia levigata
Bonia parvifloscula
Bonia solida
Bonia tonkinensis
Buergersiochloa bambusoides
Cambajuva ulei
Cathariostachys capitata
Cathariostachys madagascariensis
Cephalostachyum burmanicum
Cephalostachyum capitatum
Cephalostachyum chapelieri
Cephalostachyum chevalieri
Cephalostachyum flavescens
Cephalostachyum langbianense
Cephalostachyum latifolium
Cephalostachyum mannii
Cephalostachyum mindorense
Cephalostachyum pallidum
Cephalostachyum pergracile(6)*
Cephalostachyum perrieri
Cephalostachyum scandens
Cephalostachyum viguieri
Cephalostachyum virgatum(2)*
Chimonobambusa angustifolia(1)*
Chimonobambusa armata
Chimonobambusa arunachalensis
Chimonobambusa brevinoda
Chimonobambusa callosa
Chimonobambusa communis
Chimonobambusa convoluta
Chimonobambusa damingshanensis
Chimonobambusa fansipanensis
Chimonobambusa gracilis
Chimonobambusa grandifolia
Chimonobambusa hejiangensis(1)*
Chimonobambusa hirtinoda
Chimonobambusa hsuehiana
Chimonobambusa jainii
Chimonobambusa lactistriata
Chimonobambusa leishanensis
Chimonobambusa luzhiensis
Chimonobambusa macrophylla(2)*
Chimonobambusa marmorea(11)*
Chimonobambusa metuoensis
Chimonobambusa microfloscula
Chimonobambusa montigena
Chimonobambusa ningnanica
Chimonobambusa opienensis
Chimonobambusa pachystachys(1)*
Chimonobambusa paucispinosa
Chimonobambusa puberula
Chimonobambusa pubescens
Chimonobambusa purpurea
Chimonobambusa quadrangularis(17)*
Chimonobambusa rigidula
Chimonobambusa sichuanensis
Chimonobambusa szechuanensis(1)*
Chimonobambusa tuberculata
Chimonobambusa tumidissinoda(5)*
Chimonobambusa unifolia
Chimonobambusa utilis
Chimonobambusa verruculosa
Chimonocalamus baviensis
Chimonocalamus burmaensis
Chimonocalamus cibarius
Chimonocalamus delicatus
Chimonocalamus dumosus
Chimonocalamus fimbriatus
Chimonocalamus gallatlyi
Chimonocalamus griffithianus
Chimonocalamus longiligulatus
Chimonocalamus longispiculatus
Chimonocalamus longiusculus
Chimonocalamus lushaiensis
Chimonocalamus makuanensis
Chimonocalamus montanus
Chimonocalamus nagalandianus
Chimonocalamus pallens
Chimonocalamus peregrinus
Chimonocalamus tortuosus
Chusquea abietifolia(1)*
Chusquea acuminata
Chusquea acuminatissima
Chusquea albilanata
Chusquea amistadensis
Chusquea andina
Chusquea anelytra
Chusquea anelytroides
Chusquea angusta
Chusquea angustifolia
Chusquea annagardneriae
Chusquea antioquensis
Chusquea aperta
Chusquea arachniformis
Chusquea argentina
Chusquea aristata
Chusquea aspera
Chusquea asymmetrica
Chusquea attenuata
Chusquea aurea
Chusquea baculifera
Chusquea bahiana
Chusquea bambusoides(1)*
Chusquea barbata
Chusquea bilimekii
Chusquea bradei
Chusquea caamanoi
Chusquea caparaoensis
Chusquea capitata
Chusquea capituliflora
Chusquea ciliata
Chusquea ciliatifolia
Chusquea circinata(2)*
Chusquea clarkiae
Chusquea clemirae
Chusquea coronalis(3)*
Chusquea cortesii
Chusquea costaricensis
Chusquea culeou(5)*
Chusquea cumingii(1)*
Chusquea cylindrica
Chusquea decolorata
Chusquea deficiens(2)*
Chusquea deflexa
Chusquea delicatula
Chusquea depauperata
Chusquea diversiglumis
Chusquea dombeyana
Chusquea egluma

Chusquea elata
Chusquea enigmatica
Chusquea erecta
Chusquea exasperata
Chusquea falcata
Chusquea fasciculata
Chusquea fendleri
Chusquea fernandezia
Chusquea fimbriligulata
Chusquea floribunda
Chusquea foliosa(2)*
Chusquea galeottiana
Chusquea gigantea
Chusquea glauca
Chusquea glomerata
Chusquea gracilis
Chusquea grandiflora
Chusquea guirigayensis
Chusquea hatschbachii
Chusquea heterophylla(1)*
Chusquea huantensis
Chusquea ibiramae
Chusquea inamoena
Chusquea juergensii(1)*
Chusquea laegaardii
Chusquea lanceolata(1)*
Chusquea latifolia
Chusquea lehmannii(2)*
Chusquea leonardiorum
Chusquea leptophylla
Chusquea liebmannii
Chusquea ligulata
Chusquea linearis(3)*
Chusquea londoniae
Chusquea longifolia
Chusquea longiligulata
Chusquea longipendula
Chusquea longiprophylla
Chusquea longispiculata
Chusquea lorentziana(1)*
Chusquea loxensis
Chusquea maclurei
Chusquea macrostachya
Chusquea maculata
Chusquea magnifolia
Chusquea matlatzinca
Chusquea mayrae
Chusquea meyeriana(1)*
Chusquea microphylla
Chusquea mimosa
Chusquea mirabilis
Chusquea mollis
Chusquea montana(1)*
Chusquea mulleri
Chusquea multiramea
Chusquea nana
Chusquea nelsonii
Chusquea neurophylla
Chusquea nobilis
Chusquea nudiramea
Chusquea nutans(2)*
Chusquea oligophylla
Chusquea oxylepis
Chusquea pallida
Chusquea paludicola
Chusquea patens
Chusquea perligulata
Chusquea perotensis
Chusquea peruviana
Chusquea petiolata
Chusquea picta
Chusquea pinifolia(1)*
Chusquea pittieri
Chusquea pohlii
Chusquea polyclados
Chusquea pubispicula
Chusquea pulchella
Chusquea purdieana
Chusquea quila
Chusquea ramosissima(2)*
Chusquea renvoizei
Chusquea repens(1)*
Chusquea rigida
Chusquea riosaltensis
Chusquea robusta
Chusquea scabra
Chusquea scandens(4)*
Chusquea sclerophylla
Chusquea sellowii
Chusquea serpens
Chusquea serrulata(2)*
Chusquea silverstonei
Chusquea simpliciflora(1)*
Chusquea smithii
Chusquea sneidernii
Chusquea spadicea
Chusquea spathacea
Chusquea spectabilis
Chusquea spencei(13)*
Chusquea spicata
Chusquea straminea
Chusquea stuebelii
Chusquea subtessellata
Chusquea subtilis
Chusquea subulata
Chusquea sulcata
Chusquea talamancensis
Chusquea tarmensis
Chusquea tenella
Chusquea tenuiglumis
Chusquea tessellata(1)*
Chusquea tomentosa
Chusquea tonduzii(1)*
Chusquea tovari
Chusquea tuberculosa
Chusquea uliginosa
Chusquea uniflora
Chusquea urelytra
Chusquea valdiviensis(1)*
Chusquea villosa
Chusquea virgata
Chusquea vulcanalis
Chusquea wilkesii
Chusquea windischii
Chusquea yungasensis
Colanthelia burchellii
Colanthelia cingulata
Colanthelia distans
Colanthelia intermedia
Colanthelia lanciflora
Colanthelia macrostachya
Colanthelia rhizantha(1)*
Cryptochloa exauritus
Cryptochloa capillata(1)*
Cryptochloa concinna
Cryptochloa decumbens
Cryptochloa dressleri
Cryptochloa soderstromii
Cryptochloa strictiflora(6)*
Cryptochloa unispiculata
Cryptochloa variana
Cyrtochloa fenixii
Cyrtochloa hirsuta
Cyrtochloa luzonica
Cyrtochloa major
Cyrtochloa mindoroensis
Cyrtochloa puser
Cyrtochloa toppingii
Davidsea attenuata
Decaryochloa diadelpha
Dendrocalamus asper?(11)*
Dendrocalamus bacthaiensis
Dendrocalamus bambusoides
Dendrocalamus barbatus(1)*
Dendrocalamus bengkalisensis
Dendrocalamus birmanicus
Dendrocalamus brandisii(2)*
Dendrocalamus buar
Dendrocalamus calostachyus(1)*
Dendrocalamus cauhaiensis
Dendrocalamus cinctus
Dendrocalamus collettianus
Dendrocalamus detinens
Dendrocalamus dumosus
Dendrocalamus elegans
Dendrocalamus farinosus
Dendrocalamus fugongensis
Dendrocalamus giganteus?(15)*
Dendrocalamus hait
Dendrocalamus hamiltonii(1)*
Dendrocalamus hirtellus
Dendrocalamus hookeri
Dendrocalamus jianshuiensis
Dendrocalamus khoonmengii
Dendrocalamus latiflorus?(11)*
Dendrocalamus liboensis
Dendrocalamus longispathus(1)*
Dendrocalamus macroculmis
Dendrocalamus maiensis
Dendrocalamus manipureanus
Dendrocalamus membranaceus(4)*
Dendrocalamus menglongensis
Dendrocalamus merrillianus
Dendrocalamus messeri
Dendrocalamus minor
Dendrocalamus multiflosculus
Dendrocalamus nhatrangensis
Dendrocalamus nianhei
Dendrocalamus nudus
Dendrocalamus pachystachyus
Dendrocalamus parishii
Dendrocalamus parvigemma
Dendrocalamus peculiaris
Dendrocalamus pendulus
Dendrocalamus poilanei
Dendrocalamus pulverulentus
Dendrocalamus rugosiglumis
Dendrocalamus sahnii
Dendrocalamus sang
Dendrocalamus semiscandens
Dendrocalamus sericeus
Dendrocalamus sikkimensis
Dendrocalamus sinicus
Dendrocalamus sinuatus
Dendrocalamus somdevae
Dendrocalamus strictus†(27)*
Dendrocalamus suberosus
Dendrocalamus taybacensis
Dendrocalamus tibeticus
Dendrocalamus tomentosus
Dendrocalamus triramus
Dendrocalamus tsiangii
Dendrocalamus velutinus
Dendrocalamus wabo
Dendrocalamus xishuangbannaensis
Dendrocalamus yentuensis
Dendrocalamus yunnanicus
Diandrolyra bicolor(1)*
Diandrolyra pygmaea
Diandrolyra tatianae
Didymogonyx geminatum(1)*

Didymogonyx longispiculatum
Dinochloa acutiflora
Dinochloa alata
Dinochloa albociliata
Dinochloa andamanica
Dinochloa aopaensis
Dinochloa barbata
Dinochloa cordata
Dinochloa darvelana
Dinochloa dielsiana
Dinochloa diffusa
Dinochloa elmeri
Dinochloa erecta
Dinochloa glabrescens
Dinochloa hirsuta
Dinochloa kostermansiana
Dinochloa luconiae
Dinochloa macclellandii
Dinochloa malayana(1)*
Dinochloa matmat
Dinochloa morowaliensis
Dinochloa nicobariana
Dinochloa obclavata
Dinochloa oblonga
Dinochloa orenuda
Dinochloa palawanensis
Dinochloa petasiensis
Dinochloa prunifera
Dinochloa pubiramea
Dinochloa robusta
Dinochloa scabrida
Dinochloa scandens
Dinochloa sepang
Dinochloa sipitangensis
Dinochloa sublaevigata
Dinochloa trichogona
Dinochloa truncata
Dinochloa utilis
Drepanostachyum ampullare
Drepanostachyum annulatum
Drepanostachyum falcatum(5)*
Drepanostachyum fractiflexum
Drepanostachyum intermedium(1)*
Drepanostachyum khasianum(1)*
Drepanostachyum kurzii
Drepanostachyum membranaceum
Drepanostachyum merretii
Drepanostachyum polystachyum
Drepanostachyum semiorbiculatum
Drepanostachyum stoloniforme
Ekmanochloa aristata
Ekmanochloa subaphylla
Elytrostachys clavigera
Elytrostachys typica
Eremitis afimbriata
Eremitis magnifica
Eremitis parviflora
Eremocaulon amazonicum
Eremocaulon asymmetricum
Eremocaulon aureofimbriatum
Eremocaulon capitatum
Fargesia acuticontracta
Fargesia adpressa
Fargesia albocerea
Fargesia altior
Fargesia angustissima(1)*
Fargesia apicirubens
Fargesia boliana
Fargesia brevipes
Fargesia brevissima
Fargesia caduca
Fargesia canaliculata
Fargesia circinata
Fargesia communis
Fargesia concinna
Fargesia conferta
Fargesia contracta
Fargesia cuspidata
Fargesia daminiu
Fargesia declivis
Fargesia decurvata
Fargesia denudata(1)*
Fargesia dracocephala(4)*
Fargesia dulcicula
Fargesia dura
Fargesia edulis
Fargesia elegans
Fargesia emaculata
Fargesia emeryi
Fargesia exposita
Fargesia extensa
Fargesia fansipanensis
Fargesia farcta
Fargesia ferax(1)*
Fargesia frigida
Fargesia fungosa(3)*
Fargesia funiushanensis
Fargesia glabrifolia
Fargesia gongshanensis
Fargesia grossa
Fargesia hackelii
Fargesia hainanensis
Fargesia hsuehiana
Fargesia huizensis
Fargesia hygrophila
Fargesia jiulongensis
Fargesia lincangensis
Fargesia longiuscula
Fargesia lushuiensis
Fargesia macclureana(1)*
Fargesia mairei
Fargesia mali
Fargesia melanostachys
Fargesia murielae(6)*
Fargesia nitida(8)*
Fargesia nujiangensis
Fargesia obliqua
Fargesia orbiculata
Fargesia papyrifera
Fargesia pauciflora
Fargesia perlonga
Fargesia pleniculmis
Fargesia plurisetosa
Fargesia porphyrea
Fargesia praecipua
Fargesia qinlingensis
Fargesia robusta(4)*
Fargesia rufa(2)*
Fargesia sagittatinea
Fargesia scabrida(1)*
Fargesia schmidiana
Fargesia semicoriacea
Fargesia similaris
Fargesia solida
Fargesia spathacea(5)*
Fargesia stenoclada
Fargesia strigosa
Fargesia subflexuosa
Fargesia sylvestris
Fargesia tenuilignea
Fargesia ungulata
Fargesia utilis(3)*
Fargesia vicina
Fargesia weiningensis
Fargesia wuliangshanensis
Fargesia yajiangensis
Fargesia yuanjiangensis
Fargesia yulongshanensis
Fargesia yunnanensis
Fargesia zayuensis
Ferrocalamus fibrillosus
Ferrocalamus rimosivaginus
Ferrocalamus strictus
Filgueirasia arenicola
Filgueirasia cannavieira
Fimbribambusa horsfieldii
Fimbribambusa microcephala
Froesiochloa boutelouoides
Gaoligongshania megalothyrsa
Gelidocalamus albopubescens
Gelidocalamus annulatus
Gelidocalamus dongdingensis
Gelidocalamus kunishii
Gelidocalamus latifolius
Gelidocalamus longiinternodus
Gelidocalamus multifolius
Gelidocalamus rutilans
Gelidocalamus solidus
Gelidocalamus stellatus
Gelidocalamus subsolidus
Gelidocalamus tessellatus
Gelidocalamus velutinus
Gigantochloa achmadii
Gigantochloa albociliata(4)*
Gigantochloa albopilosa
Gigantochloa albovestita
Gigantochloa apus(5)*
Gigantochloa atroviolacea(1)*
Gigantochloa atter(1)*
Gigantochloa aya
Gigantochloa baliana
Gigantochloa balui
Gigantochloa bastareana
Gigantochloa calcicola
Gigantochloa cochinchinensis
Gigantochloa compressa(1)*
Gigantochloa densa
Gigantochloa dinhensis
Gigantochloa felix
Gigantochloa hasskarliana(5)*
Gigantochloa hayatae
Gigantochloa hirtinoda
Gigantochloa holttumiana
Gigantochloa hosseusii
Gigantochloa kuring
Gigantochloa latifolia
Gigantochloa levis(2)*
Gigantochloa ligulata
Gigantochloa longiprophylla
Gigantochloa luteostriata(1)*
Gigantochloa macrostachya
Gigantochloa magentea
Gigantochloa manggong(1)*
Gigantochloa membranoidea
Gigantochloa multiculmis
Gigantochloa multifloscula
Gigantochloa nigrociliata
Gigantochloa papyracea
Gigantochloa parvifolia
Gigantochloa poilanei
Gigantochloa pruriens
Gigantochloa pubinervis
Gigantochloa pubipetiolata
Gigantochloa ridleyi(1)*
Gigantochloa robusta(1)*
Gigantochloa rostrata
Gigantochloa scortechinii
Gigantochloa serik
Gigantochloa taluh
Gigantochloa tenuispiculata
Gigantochloa thoi
Gigantochloa tomentosa
Gigantochloa velutina

Gigantochloa verticillata(6)*
Gigantochloa vietnamica
Gigantochloa vinhphuica
Gigantochloa wallichiana
Gigantochloa wrayi(1)*
Glaziophyton mirabile
Greslania circinata
Greslania montana
Greslania multiflora
Greslania rivularis
Guadua aculeata
Guadua amplexifolia(1)*
Guadua angustifolia(6)*
Guadua calderoniana
Guadua chacoensis
Guadua chaparensis
Guadua ciliata
Guadua glomerata
Guadua incana
Guadua inermis
Guadua latifolia
Guadua lindmanii
Guadua longifolia
Guadua lynnclarkiae
Guadua macclurei
Guadua macrospiculata
Guadua macrostachya
Guadua maculosa
Guadua magna
Guadua paniculata(1)*
Guadua paraguayana
Guadua polyclados
Guadua refracta(1)*
Guadua sarcocarpa
Guadua superba
Guadua tagoara
Guadua takahashiae
Guadua trinii(5)*
Guadua uncinata
Guadua variegata
Guadua velutina
Guadua venezuelae
Guadua virgata
Guadua weberbaueri

Hickelia africana
Hickelia alaotrensis
Hickelia madagascariensis
Hickelia perrieri(1)*
Himalayacalamus asper(1)*
Himalayacalamus brevinodus
Himalayacalamus collaris
Himalayacalamus cupreus
Himalayacalamus falconeri(6)*
Himalayacalamus fimbriatus
Himalayacalamus hookerianus(1)*
Himalayacalamus planatus
Himalayacalamus porcatus(1)*
Hitchcockella baronii
Holttumochloa korbuensis
Holttumochloa magica
Holttumochloa pubescens
Indocalamus amplexicaulis
Indocalamus barbatus
Indocalamus bashanensis
Indocalamus chishuiensis
Indocalamus confertus
Indocalamus cordatus
Indocalamus decorus
Indocalamus emeiensis
Indocalamus guangdongensis
Indocalamus herklotsii
Indocalamus hirsutissimus

Indocalamus hirtivaginatus
Indocalamus hispidus
Indocalamus hunanensis
Indocalamus inaequilaterus
Indocalamus jinpingensis
Indocalamus latifolius(1)*
Indocalamus longiauritus
Indocalamus macrophyllus
Indocalamus multinervis
Indocalamus pedalis
Indocalamus petelotii
Indocalamus pseudosinicus
Indocalamus pumilus
Indocalamus quadratus
Indocalamus suichuanensis
Indocalamus tessellatus(1)*
Indocalamus tongchuensis
Indocalamus victorialis
Indocalamus youxiuensis
Indosasa angustata
Indosasa bacquangensis
Indosasa crassiflora
Indosasa gigantea
Indosasa glabrata
Indosasa hispida
Indosasa ingens
Indosasa laotica
Indosasa lipoensis
Indosasa longispicata
Indosasa lunata
Indosasa parvifolia
Indosasa patens
Indosasa shibataeaoides
Indosasa singulispicula
Indosasa sinica(1)*
Indosasa sondongensis
Indosasa spongiosa

Indosasa triangulata
Kinabaluchloa nebulosa
Kinabaluchloa wrayi
Kuruna debilis
Kuruna densifolia
Kuruna floribunda
Kuruna scandens
Kuruna walkeriana
Kuruna wightiana
Lithachne horizontalis
Lithachne humilis
Lithachne pauciflora(1)*
Lithachne pinetii
Maclurochloa montana
Maclurochloa tonkinensis
Maclurolyra tecta
Melocalamus arrectus
Melocalamus blaoensis
Melocalamus compactiflorus
Melocalamus cucphuongensis
Melocalamus elevatissimus
Melocalamus indicus
Melocalamus kbangensis
Melocalamus mastersii
Melocalamus ningmingensis
Melocalamus pacoensis
Melocalamus scandens
Melocalamus truongsonensis
Melocalamus yenbaiensis
Melocalamus yunnanensis
Melocanna baccifera(4)*
Melocanna humilis
Merostachys abadiana
Merostachys annulifera
Merostachys argentea
Merostachys argyronema
Merostachys bifurcata
Merostachys brevigluma

Merostachys brevispica
Merostachys burmanii
Merostachys calderoniana
Merostachys caucaiana
Merostachys ciliata
Merostachys claussenii
Merostachys exserta
Merostachys filgueirasii
Merostachys fimbriata
Merostachys fischeriana
Merostachys fistulosa
Merostachys glauca
Merostachys kleinii
Merostachys kunthii
Merostachys lanata
Merostachys latifolia
Merostachys leptophylla
Merostachys magellanica
Merostachys magnispicula
Merostachys maguireorum
Merostachys medullosa
Merostachys multiramea
Merostachys neesii
Merostachys pauciflora
Merostachys petiolata
Merostachys pilifera
Merostachys pluriflora
Merostachys polyantha
Merostachys procerrima
Merostachys ramosissima
Merostachys retrorsa
Merostachys riedeliana
Merostachys rondoniensis
Merostachys scandens
Merostachys sellovii
Merostachys skvortzovii
Merostachys sparsiflora
Merostachys speciosa
Merostachys tatianae
Merostachys ternata

Merostachys vestita
Merostachys yungasensis
Mniochloa pulchella
Mullerochloa moreheadiana
Myriocladus cardonae
Myriocladus churunensis
Myriocladus distantiflorus
Myriocladus exsertus
Myriocladus grandifolius
Myriocladus involutus
Myriocladus longiramosus
Myriocladus neblinaensis
Myriocladus paludicola
Myriocladus simplex
Myriocladus steyermarkii
Myriocladus virgatus
Nastus ambrensis
Nastus aristatus
Nastus borbonicus
Nastus decaryanus
Nastus elatoides
Nastus elatus(1)*
Nastus elegantissimus
Nastus elongatus
Nastus emirnensis
Nastus glaucus
Nastus holttumianus
Nastus hooglandii
Nastus humbertianus
Nastus humilus
Nastus lokohoensis
Nastus longispicula
Nastus madagascariensis
Nastus manongarivensis
Nastus obtusus
Nastus perrieri
Nastus productus
Nastus reholttumianus
Nastus rudimentifer
Nastus tsaratananensis
Neohouzeaua coradata

Neohouzeaua fimbriata
Neohouzeaua helferi
Neohouzeaua kerriana
Neohouzeaua mekongensis(1)*
Neohouzeaua puberula
Neohouzeaua stricta
Neohouzeaua tavoyana
Neololeba amahussana
Neololeba atra
Neololeba glabra
Neololeba hirsuta
Neololeba inaurita
Neomicrocalamus andropogonifolius
Neomicrocalamus clarkei
Neomicrocalamus dongvanensis
Neomicrocalamus prainii
Neomicrocalamus yunnanensis
Nianhochloa bidoupensis
Ochlandra beddomei
Ochlandra ebracteata
Ochlandra keralensis
Ochlandra scriptoria
Ochlandra setigera
Ochlandra sivagiriana
Ochlandra soderstromiana
Ochlandra spirostylis
Ochlandra stridula
Ochlandra talbotii
Ochlandra travancorica
Ochlandra wightii
Oldeania alpina(1)*
Oligostachyum bilobum
Oligostachyum exauriculatum
Oligostachyum glabrescens
Oligostachyum gracilipes
Oligostachyum hupehense
Oligostachyum lanceolatum
Oligostachyum lubricum(1)*
Oligostachyum nuspiculum
Oligostachyum oedogonatum
Oligostachyum paniculatum
Oligostachyum puberulum
Oligostachyum scabriflorum
Oligostachyum scopulum
Oligostachyum shiuyingianum
Oligostachyum spongiosum
Oligostachyum sulcatum
Oligostachyum wuyishanicum
Oligostachyum yongangense
Olmeca clarkiae
Olmeca fulgor
Olmeca recta
Olmeca reflexa
Olmeca zapotecorum
Olyra amapana
Olyra buchtienii
Olyra caudata
Olyra ciliatifolia
Olyra davidseana
Olyra ecaudata
Olyra fasciculata
Olyra filiformis
Olyra glaberrima(1)*
Olyra holttumiana
Olyra humilis
Olyra juruana
Olyra latifolia?(2)*
Olyra latispicula
Olyra longifolia
Olyra loretensis
Olyra maranonensis
Olyra obliquifolia
Olyra retrorsa
Olyra standleyi(1)*
Olyra tamanquareana
Olyra taquara
Olyra wurdackii
Oreobambos buchwaldii
Otatea acuminata(2)*
Otatea carrilloi
Otatea fimbriata
Otatea glauca(1)*
Otatea ramirezii
Otatea reynosoana
Otatea transvolcanica
Otatea ximenae
Oxytenanthera abyssinica(6)*
Parabambusa kainii
Pariana argentea
Pariana aurita
Pariana bicolor
Pariana campestris
Pariana carvalhoi
Pariana concinna
Pariana distans
Pariana ecuadorensis
Pariana gracilis
Pariana lanceolata
Pariana ligulata
Pariana maynensis
Pariana modesta
Pariana multiflora
Pariana nervata
Pariana obtusa
Pariana ovalifolia
Pariana pallida
Pariana parvispica
Pariana radiciflora
Pariana setosa
Pariana simulans
Pariana sociata
Pariana stenolemma
Pariana strigosa
Pariana swallenii
Pariana tenuis
Pariana trichosticha
Pariana ulei
Pariana velutina
Parodiolyra aratitiyopensis
Parodiolyra colombiensis
Parodiolyra lateralis
Parodiolyra luetzelburgii
Parodiolyra micrantha(1)*
Parodiolyra ramosissima
Perrierbambus incarnata(1)*
Perrierbambus madagascariensis
Perrierbambus tsarasaotrensis
Phuphanochloa speciosa
Phyllosasa tranquillans
Phyllostachys acuta(4)*
Phyllostachys acutiligula
Phyllostachys angusta(1)*
Phyllostachys arcana(4)*
Phyllostachys atrovaginata(2)*
Phyllostachys aurea†(45)*
Phyllostachys aureosulcata(6)*
Phyllostachys bambusoides†(6)*
Phyllostachys bissetii(5)*
Phyllostachys carnea
Phyllostachys circumpilis(1)*
Phyllostachys compressus
Phyllostachys corrugata
Phyllostachys dulcis(4)*
Phyllostachys edulis†(15)*
Phyllostachys elegans
Phyllostachys fimbriligula
Phyllostachys flexuosa†(9)*
Phyllostachys glabrata(1)*
Phyllostachys glauca(4)*
Phyllostachys guizhouensis
Phyllostachys heteroclada(2)*
Phyllostachys hirtivagina
Phyllostachys kwangsiensis
Phyllostachys lofushanensis(1)*
Phyllostachys makinoi(1)*
Phyllostachys mannii(4)*
Phyllostachys meyeri(5)*
Phyllostachys mirabilis
Phyllostachys nidularia(7)*
Phyllostachys nigella(1)*
Phyllostachys nigra†(26)*
Phyllostachys nuda(7)*
Phyllostachys parvifolia
Phyllostachys pierreana
Phyllostachys platyglossa
Phyllostachys prominens
Phyllostachys propinqua(1)*
Phyllostachys purpureociliata
Phyllostachys reticulata
Phyllostachys rivalis(2)*
Phyllostachys robustiramea(1)*
Phyllostachys rubicunda
Phyllostachys rubromarginata(4)*
Phyllostachys rutila
Phyllostachys shuchengensis
Phyllostachys stimulosa(3)*
Phyllostachys sulphurea(6)*
Phyllostachys tianmuensis
Phyllostachys varioauriculata
Phyllostachys veitchiana
Phyllostachys verrucosa
Phyllostachys violascens(5)*
Phyllostachys virella
Phyllostachys viridiglaucescens(7)*
Phyllostachys vivax(6)*
Phyllostachys yunhoensis
Pinga marginata
Piresia goeldii
Piresia leptophylla
Piresia macrophylla
Piresia palmula
Piresia sympodica
Piresiella strephioides
Pleioblastus albosericeus
Pleioblastus altiligulatus
Pleioblastus amarus
Pleioblastus argenteostriatus†(22)*
Pleioblastus chino(1)*
Pseudosasa distichus†(4)*
Pleioblastus gozadakensis
Pleioblastus gramineus(6)*
Pleioblastus guilongshanensis
Pleioblastus hattorianus
Pleioblastus hsienchuensis
Pseudosasa humilis†(8)*
Pleioblastus incarnatus
Pleioblastus intermedius

Pleioblastus juxianensis
Pleioblastus kodzumae
Pleioblastus kongosanensis
Pleioblastus linearis(3)*
Pleioblastus maculatus
Pleioblastus maculosoides
Pleioblastus matsunoi
Pleioblastus nagashima(3)*
Pleioblastus oleosus
Pleioblastus patellaris
Pleioblastus pseudocommunis
Pleioblastus pseudosasaoides
Pleioblastus rugatus
Pleioblastus sanmingensis
Pleioblastus simonii?(15)*
Pleioblastus solidus
Pleioblastus truncatus
Pleioblastus variegatus(12)*
Pleioblastus wuyishanensis(1)*
Pleioblastus yamadorianus
Pleioblastus yixingensis
Pseudobambusa schizostachyoides
Pseudosasa aeria
Pseudosasa amabilis(2)*
Pseudosasa amplexicaulis
Pseudosasa brevivaginata
Pseudosasa cantorii(1)*
Pseudosasa gracilis
Pseudosasa hindsii(8)*
Pseudosasa japonica?(23)*
Pseudosasa jiangleensis
Pseudosasa longiligula
Pseudosasa maculifera
Pseudosasa membraniligulata
Pseudosasa nabeshimana
Pseudosasa orthotropa
Pseudosasa owatarii
Pseudosasa pubiflora
Pseudosasa subsolida
Pseudosasa viridula
Pseudosasa wuyiensis
Pseudosasa zhongyanensis
Pseudostachyum polymorphum(1)*
Pseudostachyum wakha
Pseudoxytenanthera bourdillonii
Pseudoxytenanthera monadelpha
Pseudoxytenanthera parvifolia
Pseudoxytenanthera ritcheyi
Pseudoxytenanthera stocksii
Racemobambos celebica
Racemobambos ceramica
Racemobambos congesta
Racemobambos gibbsiae
Racemobambos glabra
Racemobambos hepburnii
Racemobambos hirsuta
Racemobambos hirta
Racemobambos holttumii
Racemobambos kutaiensis
Racemobambos multiramosa
Racemobambos novohibernica
Racemobambos pairinii
Racemobambos raynalii
Racemobambos rigidifolia
Racemobambos rupicola
Racemobambos schultzei
Racemobambos sessilis
Racemobambos setifera
Raddia angustifolia
Raddia brasiliensis
Raddia distichophylla
Raddia guianensis
Raddia lancifolia
Raddia megaphylla
Raddia portoi
Raddia soderstromii
Raddia stolonifera
Raddiella esenbeckii(1)*
Raddiella kaieteurana
Raddiella lunata
Raddiella malmeana
Raddiella minima
Raddiella molliculma
Raddiella potaroensis
Raddiella vanessiae
Rehia nervata
Reitzia smithii
Rhipidocladum abregoense
Rhipidocladum ampliflorum
Rhipidocladum angustiflorum
Rhipidocladum arenicola
Rhipidocladum bartlettii
Rhipidocladum clarkiae
Rhipidocladum cordatum
Rhipidocladum harmonicum
Rhipidocladum martinezii
Rhipidocladum maxonii
Rhipidocladum neumannii
Rhipidocladum pacuarense
Rhipidocladum panamense
Rhipidocladum parviflorum
Rhipidocladum pittieri
Rhipidocladum prestoei
Rhipidocladum racemiflorum
Rhipidocladum rubrofimbriatum
Rhipidocladum sibilans
Sarocalamus faberi
Sarocalamus racemosus
Sarocalamus spanostachyus
Sasa bitchuensis(1)*
Sasa cernua
Sasa chartacea
Sasa elegantissima(2)*
Sasa fugeshiensis
Sasa gracillima
Sasa guangdongensis
Sasa guangxiensis
Sasa hainanensis
Sasa hayatae
Sasa heterotricha
Sasa hibaconuca
Sasa hidaensis
Sasa hisauchii
Sasa kagamiana
Sasa kanayamensis
Sasa kogasensis
Sasa kurilensis(1)*
Sasa kurokawana
Sasa longiligulata
Sasa magnifica
Sasa magnonoda
Sasa masamuneana(3)*
Sasa megalogluma
Sasa megalophylla
Sasa miakeana
Sasa minensis
Sasa nipponica(1)*
Sasa oblongula
Sasa occidentalis
Sasa oshidensis
Sasa palmata(13)*
Sasa pubens
Sasa pubiculmis
Sasa pulcherrima
Sasa quelpaertensis(1)*
Sasa ramosa(6)*
Sasa rubrovaginata
Sasa sadoensis
Sasa samaniana
Sasa scytophylla
Sasa senanensis(2)*
Sasa septentrionalis
Sasa shimidzuana
Sasa sirakurensis
Sasa subglabra
Sasa subvillosa
Sasa suzukii
Sasa takizawana
Sasa tatewakiana
Sasa tenuifolia
Sasa tokugawana
Sasa tomentosa
Sasa tsuboiana(2)*
Sasa tsukubensis
Sasa veitchii(9)*
Sasa yahikoensis
Sasaella bitchuensis
Sasaella caudiceps
Sasaella hidaensis
Sasaella hisauchii
Sasaella iwatekensis
Sasaella kogasensis
Sasaella leucorhoda
Sasaella masamuneana
Sasaella ovarifolia
Sasaella ramosa
Sasaella sadoensis
Sasaella shiobarensis
Sasamorpha borealis(2)*
Sasamorpha hubeiensis
Sasamorpha oshidensis
Sasamorpha qingyuanensis
Sasamorpha sinica(1)*
Schizostachyum aciculare
Schizostachyum aequiramosum
Schizostachyum alopecurus
Schizostachyum andamanicum
Schizostachyum atrocingulare
Schizostachyum auriculatum
Schizostachyum bamban
Schizostachyum blumei
Schizostachyum brachycladum(2)*
Schizostachyum brachythyrsus
Schizostachyum castaneum
Schizostachyum caudatum
Schizostachyum chinense
Schizostachyum copelandii
Schizostachyum cornutum
Schizostachyum curranii
Schizostachyum cuspidatum
Schizostachyum diaoluoshanense
Schizostachyum distans
Schizostachyum dullooa
Schizostachyum dumetorum(2)*
Schizostachyum flexuosum
Schizostachyum funghomii(1)*
Schizostachyum glaucifolium(3)*
Schizostachyum glaucocladum
Schizostachyum gracile
Schizostachyum grande
Schizostachyum hainanense
Schizostachyum hantu
Schizostachyum insulare

Schizostachyum iraten
Schizostachyum jaculans(2)*
Schizostachyum kalpongianum
Schizostachyum khoonmengii
Schizostachyum latifolium
Schizostachyum lengguanii
Schizostachyum lima(1)*
Schizostachyum lumampao(2)*
Schizostachyum lutescens
Schizostachyum mampouw
Schizostachyum mannii
Schizostachyum nghianum
Schizostachyum ninhthuanense
Schizostachyum perrieri
Schizostachyum pilosum
Schizostachyum pingbianense
Schizostachyum pleianthemum
Schizostachyum pseudolima(1)*
Schizostachyum rogersii
Schizostachyum sanguineum
Schizostachyum seshagirianum
Schizostachyum silicatum
Schizostachyum terminale
Schizostachyum tessellatum
Schizostachyum textorium
Schizostachyum undulatum
Schizostachyum wanshishanense
Schizostachyum whitei
Schizostachyum yalyense
Schizostachyum zollingeri(1)*
Shibataea chiangshanensis
Shibataea chinensis(2)*
Shibataea hispida(1)*
Shibataea kumasasa(9)*
Shibataea lancifolia(1)*
Shibataea nanpingensis
Shibataea strigosa
Sinobambusa baccanensis
Sinobambusa farinosa
Sinobambusa glabrata
Sinobambusa henryi
Sinobambusa humila
Sinobambusa incana
Sinobambusa intermedia(2)*
Sinobambusa nephroaurita
Sinobambusa rubroligula(3)*
Sinobambusa sat
Sinobambusa seminuda
Sinobambusa solearis
Sinobambusa tootsik(6)*
Sinobambusa yixingensis
Sirochloa parvifolia
Soejatmia ridleyi
Sphaerobambos hirsuta
Sphaerobambos philippinensis
Sphaerobambos subtilis
Stapletonia arunachalensis
Sucrea maculata
Sucrea monophylla
Sucrea sampaiana
Teinostachyum beddomei
Teinostachyum griffithii
Temburongia simplex
Temochloa liliana
Thamnocalamus chigar
Thamnocalamus spathiflorus(5)*
Thamnocalamus unispiculatus
Thyrsostachys oliveri(1)*
Thyrsostachys siamensis(3)*
Valiha diffusa
Valiha perrieri
Vietnamocalamus catbaensis
Vietnamosasa ciliata
Vietnamosasa darlacensis
Vietnamosasa pusilla
Yushania addingtonii
Yushania ailuropodina
Yushania anceps(7)*
Yushania andropogonoides
Yushania angustifolia
Yushania auctiaurita
Yushania baishanzuensis
Yushania basihirsuta
Yushania bojieiana
Yushania brevipaniculata(1)*
Yushania brevis
Yushania burmanica
Yushania canoviridis
Yushania cartilaginea
Yushania cava
Yushania chingii
Yushania collina
Yushania complanata
Yushania confusa
Yushania crassicollis
Yushania crispata
Yushania dafengdingensis
Yushania donganensis
Yushania elegans
Yushania elevata
Yushania exilis
Yushania falcatiaurita
Yushania farcticaulis
Yushania farinosa
Yushania flexa
Yushania glandulosa
Yushania glauca
Yushania grammata
Yushania hirsuta
Yushania hirticaulis
Yushania humbertii
Yushania lacera
Yushania laetevirens
Yushania levigata
Yushania linearis
Yushania lineolata
Yushania longiaurita
Yushania longissima(6)*
Yushania longiuscula
Yushania mabianensis
Yushania maculata
Yushania madagascariensis
Yushania maling(1)*
Yushania menghaiensis
Yushania microphylla
Yushania mitis
Yushania multiramea
Yushania niitakayamensis(4)*
Yushania oblonga
Yushania pachyclada
Yushania pantlingii
Yushania pauciramificans
Yushania perrieri
Yushania polytricha
Yushania punctulata
Yushania qiaojiaensis
Yushania rigidula
Yushania rolloana
Yushania rugosa
Yushania shangrilaensis
Yushania straminea
Yushania suijiangensis
Yushania tenuicaulis
Yushania tessellata
Yushania uniramosa
Yushania varians
Yushania velutina
Yushania vigens
Yushania violascens
Yushania wardii
Yushania weixiensis
Yushania wuyishanensis
Yushania xizangensis
Yushania yadongensis
Yushania yongdeensis

File S2.2. List of named bamboo species that did not match our accepted species list and the changes made to include or exclude them from the review database. Synonyms and spelling mistakes were updated accordingly, and unknown names were excluded.

Name used in records	Updated name	Issue
Arundinaria amabilis	*Pseudosasa amabilis*	Synonym
Arundinaria debilis	*Kuruna debilis*	Synonym
Arundinaria densifolia	*Kuruna densifolia*	Synonym
Arundinaria faberi	*Sarocalamus faberi*	Synonym
Arundinaria fargesii	*Bashania fargesii*	Synonym
Arundinaria floribunda	*Kuruna floribunda*	Synonym
Arundinaria funghomii	*Pseudosasa cantorii*	Synonym
Arundinaria graminea	*Pleioblastus gramineus*	Synonym
Arundinaria hindsii	*Pseudosasa hindsii*	Synonym
Arundinaria hookeriana	*Himalayacalamus hookerianus*	Synonym
Arundinaria humilis	*Pseudosasa humilis*	Synonym
Arundinaria japonica	*Pseudosasa japonica*	Synonym
Arundinaria kodzumae	*Pleioblastus kodzumae*	Synonym
Arundinaria kongosanensis	*Pleioblastus kongosanensis*	Synonym
Arundinaria linearis	*Pleioblastus linearis*	Synonym
Arundinaria matsunoi	*Pleioblastus matsunoi*	Synonym
Arundinaria nagashima	*Pleioblastus nagashima*	Synonym
Arundinaria nitida	*Fargesia nitida*	Synonym
Arundinaria pygmaea	*Pleioblastus variegatus*	Synonym
Arundinaria qingchengshanensis	*Bashania qingchengshanensis*	Synonym
Arundinaria racemosa	*Sarocalamus racemosus*	Synonym
Arundinaria scandens	*Kuruna scandens*	Synonym
Arundinaria shiobarensis	*Sasaella shiobarensis*	Synonym
Arundinaria simonii	*Pleioblastus simonii*	Synonym
Arundinaria spanostachya	*Sarocalamus spanostachyus*	Synonym
Arundinaria usawai	*Pseudosasa japonica*	Synonym
Arundinaria variegata	*Pleioblastus variegatus*	Synonym
Arundinaria viridistriata	*Pleioblastus variegatus*	Synonym
Arundinaria viridi-striata	*Pleioblastus variegatus*	Synonym
Arundinaria walkeriana	*Kuruna walkeriana*	Synonym
Arundinaria wightiana	*Kuruna wightiana*	Synonym
Aulonemia clarkiae	*Olmeca clarkiae*	Synonym
Aulonemia fulgor	*Olmeca fulgor*	Synonym
Bambusa amplexifolia	*Guadua amplexifolia*	Synonym
Bambusa argenteostriata	*Pleioblastus argenteostriatus*	Synonym
Bambusa arundinacea	*Bambusa bambos*	Synonym
Bambusa aurea	*Phyllostachys aurea*	Synonym
Bambusa castilloni	*Phyllostachys bambusoides*	Synonym
Bambusa glaucescens	*Bambusa multiplex*	Synonym
Bambusa guadua	*Guadua angustifolia*	Synonym
Bambusa horsfieldii	*Fimbribambusa horsfieldii*	Synonym
Bambusa microcephala	*Fimbribambusa microcephala*	Synonym
Bambusa moreheadiana	*Mullerochloa moreheadiana*	Synonym
Bambusa nana	*Bambusa multiplex*	Synonym
Bambusa paniculata	*Sasa senanensis*	Synonym
Bambusa pygmaea	*Pleioblastus variegatus*	Synonym
Bambusa shimadai	*Bambusa multiplex*	Synonym
Bambusa ventricosa	*Bambusa tuldoides*	Synonym
Chimonobambusa falcata	*Drepanostachyum falcatum*	Synonym
Dendrocalamus beecheyana	*Bambusa beecheyana*	Synonym
Dendrocalamus latifolius	*Dendrocalamus latiflorus*	Synonym
Drepanostachyum asper	*Himalayacalamus asper*	Synonym
Drepanostachyum porcatum	*Himalayacalamus porcatus*	Synonym

Eremocaulon setosum	*Aulonemia setosa*	Synonym
Gigantochloa parviflora	*Gigantochloa parvifolia*	Synonym
Gigantochloa pseudoarundinacea	*Gigantochloa verticillata*	Synonym
Greslania circinnata	*Greslania circinata*	Synonym
Indocalamus wilsonii	*Indocalamus wilsonii*	Synonym
Leleba oldhami	*Bambusa oldhamii*	Synonym
Leleba shimadai	*Bambusa multiplex*	Synonym
Melocanna arundina	*Melocanna humilis*	Synonym
Melocanna virgata	*Cephalostachyum virgatum*	Synonym
Melocanna zollingeri	*Schizostachyum zollingeri*	Synonym
Mniochloa strephioides	*Piresiella strephioides*	Synonym
Neurolepis angusta	*Chusquea angusta*	Synonym
Neurolepis aperta	*Chusquea spectabilis*	Synonym
Neurolepis aristata	*Chusquea aristata*	Synonym
Neurolepis asymmetrica	*Chusquea asymmetrica*	Synonym
Neurolepis diversiglumis	*Chusquea diversiglumis*	Synonym
Neurolepis elata	*Chusquea elata*	Synonym
Neurolepis fimbriligulata	*Chusquea fimbriligulata*	Synonym
Neurolepis glomerata	*Chusquea glomerata*	Synonym
Neurolepis laegaardii	*Chusquea laegaardii*	Synonym
Neurolepis mollis	*Chusquea mollis*	Synonym
Neurolepis nana	*Chusquea nana*	Synonym
Neurolepis petiolata	*Chusquea petiolata*	Synonym
Neurolepis pittieri	*Chusquea pittieri*	Synonym
Neurolepis rigida	*Chusquea rigida*	Synonym
Neurolepis silverstonei	*Chusquea silverstonei*	Synonym
Neurolepis villosa	*Chusquea villosa*	Synonym
Neurolepis virgata	*Chusquea virgata*	Synonym
Olyra bahiensis	*Arberella bahiensis*	Synonym
Olyra micrantha	*Parodiolyra micrantha*	Synonym
Otatea aztecorum	*Otatea acuminata*	Synonym
Pariana gleasonii	*Pariana radiciflora*	Synonym
Pariana intermedia	*Pariana campestris*	Synonym
Pariana interrupta	*Pariana campestris*	Synonym
Pariana longiflora	*Pariana radiciflora*	Synonym
Pariana lunata	*Pariana campestris*	Synonym
Pariana vulgaris	*Pariana radiciflora*	Synonym
Phyllostachys heterocycla	*Phyllostachys edulis*	Synonym
Phyllostachys praecox	*Phyllostachys violascens*	Synonym
Phyllostachys pubescens	*Phyllostachys edulis*	Synonym
Phyllostachys quilioi	*Phyllostachys bambusoides*	Synonym
Phyllostachys viridis	*Phyllostachys sulphurea*	Synonym
Pleioblastus fortunei	*Pleioblastus variegatus*	Synonym
Pleioblastus hindsii	*Pseudosasa hindsii*	Synonym
Pleioblastus humilis	*Pseudosasa humilis*	Synonym
Pleioblastus pygmaeus	*Pleioblastus variegatus*	Synonym
Pleioblastus shibuyanus	*Pleioblastus variegatus*	Synonym
Pleioblastus tsukubensis	*Sasa tsukubensis*	Synonym
Pleioblastus viridistriatus	*Bambusa viridis*	Synonym
Pseudosasa disticha	*Pseudosasa distichus*	Synonym
Pseudosasa usawai	*Pseudosasa japonica*	Synonym
Pseudoxytenanthera albociliata	*Gigantochloa albociliata*	Synonym
Rhipidocladum geminatum	*Didymogonyx geminatum*	Synonym
Rhipidocladum longispiculatum	*Didymogonyx longispiculatum*	Synonym
Sasa admirabilis	*Sasa elegantissima*	Synonym
Sasa argenteostriata	*Pleioblastus argenteostriatus*	Synonym
Sasa borealis	*Sasamorpha borealis*	Synonym
Sasa fortunei	*Pleioblastus variegatus*	Synonym
Sasa hubeiensis	*Sasamorpha hubeiensis*	Synonym
Sasa qingyuanensis	*Sasamorpha qingyuanensis*	Synonym
Sasa sinica	*Sasamorpha sinica*	Synonym
Sasa tessellata	*Indocalamus tessellatus*	Synonym

Sasaella glabra	*Sasa masamuneana*	Synonym
Schizostachyum arunachalensis	*Stapletonia arunachalensis*	Synonym
Schizostachyum beddomei	*Teinostachyum beddomei*	Synonym
Schizostachyum diffusum	*Dinochloa diffusa*	Synonym
Schizostachyum griffithii	*Teinostachyum griffithii*	Synonym
Schizostachyum polymorphum	*Pseudostachyum polymorphum*	Synonym
Semiarundinaria densiflora	*Semiarundinaria densiflora*	Synonym
Semiarundinaria fastuosa	*Semiarundinaria fastuosa*	Synonym
Semiarundinaria fortis	*Semiarundinaria fortis*	Synonym
Semiarundinaria kagamiana	*Semiarundinaria kagamiana*	Synonym
Semiarundinaria shapoensis	*Semiarundinaria shapoensis*	Synonym
Semiarundinaria sinica	*Semiarundinaria sinica*	Synonym
Semiarundinaria yashadake	*Semiarundinaria yashadake*	Synonym
Shibataea lanceifolia	*Shibataea lancifolia*	Synonym
Sinobambusa kunishii	*Gelidocalamus kunishii*	Synonym
Sinocalamus latiflorus	*Dendrocalamus latiflorus*	Synonym
Thamnocalamus falconeri	*Himalayacalamus falconeri*	Synonym
Thamnocalamus nitidus	*Fargesia nitida*	Synonym
Thamnocalamus spathaceus	*Fargesia spathacea*	Synonym
Thamnocalamus tessellatus	*Bergbambos tessellata*	Synonym
Yushania alpina	*Oldeania alpina*	Synonym
Arundinaria caudiceps	*Sasaella caudiceps*	Synonym
Arundinaria chino	*Pleioblastus argenteostriatus*	Synonym
Gigantochloa parviflora	*Gigantochloa parvifolia*	Spelling
Greslania circinnata	*Greslania circinata*	Spelling
Guadua angus	*Guadua angustifolia*	Spelling
Indocalamus wilsonii	*Indocalamus wilsonii*	Spelling
Merostachys cauciana	*Merostachys caucaiana*	Spelling
Pariana ecuadoriensis	*Pariana ecuadorensis*	Spelling
Parodiolyra columbiensis	*Parodiolyra colombiensis*	Spelling
Pleioblastus gramineaus	*Pleioblastus gramineus*	Spelling
Pleioblastus humili	*Pleioblastus humilis*	Spelling
Pleioblastus viridistriatus	*Bambusa viridis*	Spelling
Rhipidocladum abregoensis	*Rhipidocladum abregoense*	Spelling
Schizostachyum blumii	*Schizostachyum blumei*	Spelling
Shibataea kumasaca	*Shibataea kumasasa*	Spelling
Shibataea lanceifolia	*Shibataea lancifolia*	Spelling
Yushania grummata	*Yushania grammata*	Spelling
Yushania suijangensis	*Yushania suijiangensis*	Spelling
Arthrostylidium multispicatum		Unknown name/ excluded
Arundinaria auricom		Unknown name/ excluded
Arundinaria fansipanensis		Unknown name/ excluded
Arundinaria munsuensis		Unknown name/ excluded
Arundinaria pseudosasaoides		Unknown name/ excluded
Aulonemia fimbriatifolia		Unknown name/ excluded
Aulonemia sodiroana		Unknown name/ excluded
Aulonemia ulei		Unknown name/ excluded
Bambusa schizostachyoides		Unknown name/ excluded
Bonia saxatilis		Unknown name/ excluded
Drepanostachyum exauritum		Unknown name/ excluded
Fargesia chigar		Unknown name/ excluded

Indocalamus sinicus	Unknown name/ excluded
Kinabaluchloa ridleyi	Unknown name/ excluded
Myriocladus maguirei	Unknown name/ excluded
Nastus schlechteri	Unknown name/ excluded
Nastus schmutzii	Unknown name/ excluded
Phyllostachys humilis	Unknown name/ excluded
Phyllostachys octandra	Unknown name/ excluded
Pleioblastus auricomus	Unknown name/ excluded
Pseudosasa hamadae	Unknown name/ excluded
Sasa mollissima	Unknown name/ excluded
Schizostachyum biflorum	Unknown name/ excluded
Sinoarundinaria falcata	Unknown name/ excluded
Sinocalamus oldhammi	Unknown name/ excluded

File S3. List of references for bamboo invasions and the locality ('Country/ Region') of the reported invasion. The 'Database/ Report' indicates where references were originally retrieved. All references were vetted for validity on the invasion claim (see Richardson et al. 2011), 'Reference Status' indicates which references were included or excluded in the global review.

Species	Country/ Region	Database/ Report	Reference Status	Reference
Phyllostachys aurea	Australia	Pacific Island Ecosystems at Risk (PIER)	Included	(Queensland Herbarium 2002)
Phyllostachys aurea	Brazil	A Global Compendium of Weeds (Randall, 2012)	Included	(IABIN 2012)
Bambusa textilis	Brazil	A Global Compendium of Weeds (Randall, 2012)	Included	(IABIN 2008)
Bambusa vulgaris	Brazil	A Global Compendium of Weeds (Randall, 2012)	Included	(IABIN 2012)
Bambusa bambos	Cuba	Invasive Species Compendium (CABI)	Included	(Oviendo 2012)
Bambusa vulgaris	Cuba	Invasive Species Compendium (CABI)	Included	(Oviendo 2012)
Dendrocalamus strictus	Cuba	Invasive Species Compendium (CABI)	Included	(Oviendo 2012)
Phyllostachys aurea	Cuba	Invasive Species Compendium (CABI)	Included	(Oviendo 2012)
Phyllostachys bambusoides	Cuba	Invasive Species Compendium (CABI)	Included	(Oviendo 2012)
Phyllostachys flexuosa	Cuba	Invasive Species Compendium (CABI)	Included	(Oviendo 2012)
Pleioblastus argenteostriatus	Georgia	A Global Compendium of Weeds (Randall, 2012)	Included	(Kikodze 2010)
Pseudosasa distichus	Georgia	A Global Compendium of Weeds (Randall, 2012)	Included	(Kikodze 2010)
Pseudosasa humilis	Georgia	A Global Compendium of Weeds (Randall, 2012)	Included	(Kikodze 2010)
Phyllostachys aurea	Hawaii	Pacific Island Ecosystems at Risk (PIER)	Included	(Staples et al. 2002)
Phyllostachys nigra	Hawaii	Pacific Island Ecosystems at Risk (PIER)	Included	(Wagner et al. 1999; Tunison et al. 2000)
Bambusa vulgaris	Jamaica	A Global Compendium of Weeds (Randall, 2012)	Included	(Kairo et al. 2003)
Phyllostachys edulis	Japan	A Global Compendium of Weeds (Randall, 2012)	Included	(Toshiya 2004)
Phyllostachys aurea	New Zealand	Pacific Island Ecosystems at Risk (PIER)	Included	(Edgar & Connor, 2000)
Bambusa vulgaris	Puerto Rico	Invasive Species Compendium (CABI)	Included	(Blundell et al. 2003)
Dendrocalamus strictus	Puerto Rico	A Global Compendium of Weeds (Randall, 2012)	Included	(Kairo et al. 2003)
Bambusa vulgaris	Trinidad and Tobago	A Global Compendium of Weeds (Randall, 2012)	Included	(Kairo et al. 2003)
Phyllostachys aurea	United States	A Global Compendium of Weeds (Randall, 2012)	Included	(Bargeron 2003; Swearingen et al. 2010; Gucker 2009)
Bambusa balcooa	Australia	A Global Compendium of Weeds (Randall, 2012)	Not included	(Keighery & Keighery 2009)
Bambusa vulgaris	Costa Rica	Invasive Species Compendium (CABI)	Not included	(Chacón & Saborío, 2012)
Bambusa vulgaris	Galapagos Is.	Invasive Species Compendium (CABI)	Not included	(Charles Darwin Foundation 2014)
Phyllostachys aurea	Japan	A Global Compendium of Weeds (Randall, 2012)	Not included	(Toshiya 2004)
Phyllostachys nigra	Japan	A Global Compendium of Weeds (Randall, 2012)	Not included	(Toshiya 2004)
Bambusa multiplex	Reunion Is.	Pacific Island Ecosystems at Risk (PIER)	Not included	(Lavergne 2006)
Bambusa vulgaris	Reunion Is.	Pacific Island Ecosystems at Risk (PIER)	Not included	(Lavergne 2006)
Phyllostachys aurea	Reunion Is.	Pacific Island Ecosystems at Risk (PIER)	Not included	(Lavergne 2006)

Phyllostachys nigra	Reunion Is.	Pacific Island Ecosystems at Risk (PIER)	Not included	(Lavergne 2006)
Pleioblastus fortunei	United States	A Global Compendium of Weeds (Randall, 2012)	Not included	(Anon 2005)
Phyllostachys flexuosa	New Caledonia	Pacific Island Ecosystems at Risk (PIER)	Not included	(MacKee 1994)
Bambusa vulgaris	Australia	A Global Compendium of Weeds (Randall, 2012)	Not included	(Anon. 2009; Randall 2007)
Phyllostachys bambusoides	Australia	A Global Compendium of Weeds (Randall, 2012)	Not included	(Randall 2007; Anon 2009)
Phyllostachys edulis	Australia	Independent search	Not included	(Randall 2007)
Phyllostachys nigra	Australia	Pacific Island Ecosystems at Risk (PIER)	Not included	(Randall 2007; Csurhes & Edwards, 1998)
Bambusa vulgaris	Cook Is.	Pacific Island Ecosystems at Risk (PIER)	Not included	(Space & Flynn 2002)
Phyllostachys bissetii	Cook Is.	Pacific Island Ecosystems at Risk (PIER)	Not included	(Space & Flynn 2002)
Bambusa vulgaris	Costa Rica	A Global Compendium of Weeds (Randall, 2012)	Not included	(IABIN, 2008)
Bambusa vulgaris	Federated States of Micronesia	Pacific Island Ecosystems at Risk (PIER)	Not included	(Fosberg et al. 1987)
Bambusa vulgaris	Fiji	Pacific Island Ecosystems at Risk (PIER)	Not included	(Smith 1979)
Bambusa vulgaris	Guadeloupe	Independent search	Not included	(DEAL, 2011)
Bambusa vulgaris	Madagascar	A Global Compendium of Weeds (Randall, 2012)	Not included	(eFlora 2006)
Bambusa vulgaris	Martinique	Independent search	Not included	(DEAL, 2011)
Bambusa vulgaris	Mayotte Is.	Pacific Island Ecosystems at Risk (PIER)	Not included	(Comité français 2013)
Bambusa vulgaris	Mexico	A Global Compendium of Weeds (Randall, 2012)	Not included	(Conabio 2006)
Phyllostachys aurea	Mexico	A Global Compendium of Weeds (Randall, 2012)	Not included	(Conabio 2006)
Bambusa balcooa	Namibia	A Global Compendium of Weeds (Randall, 2012)	Not included	(Bethune et al. 2004)
Bambusa vulgaris	New Caledonia	Independent search	Not included	(Heque et al. 2009)
Bambusa multiplex	New Zealand	Pacific Island Ecosystems at Risk (PIER)	Not included	(Edgar & Connor, 2000)
Bambusa vulgaris	New Zealand	Invasive Species Compendium (CABI)	Not included	(Edgar & Connor, 2000)
Phyllostachys nigra	New Zealand	Pacific Island Ecosystems at Risk (PIER)	Not included	(Edgar & Connor, 2000)
Bambusa vulgaris	Niue	Invasive Species Compendium (CABI)	Not included	(Space et al. 2004)
Bambusa vulgaris	Tonga	Pacific Island Ecosystems at Risk (PIER)	Not included	(Space & Flynn 2001)
Bambusa vulgaris	United States	Independent search	Not included	(Swearingen et al. 2010)
Pseudosasa japonica	United States	Independent search	Not included	(Swearingen et al. 2010)
Bambusa vulgaris	Wallis-Futana Is.	Pacific Island Ecosystems at Risk (PIER)	Not included	(Morat & Veillon 1985)

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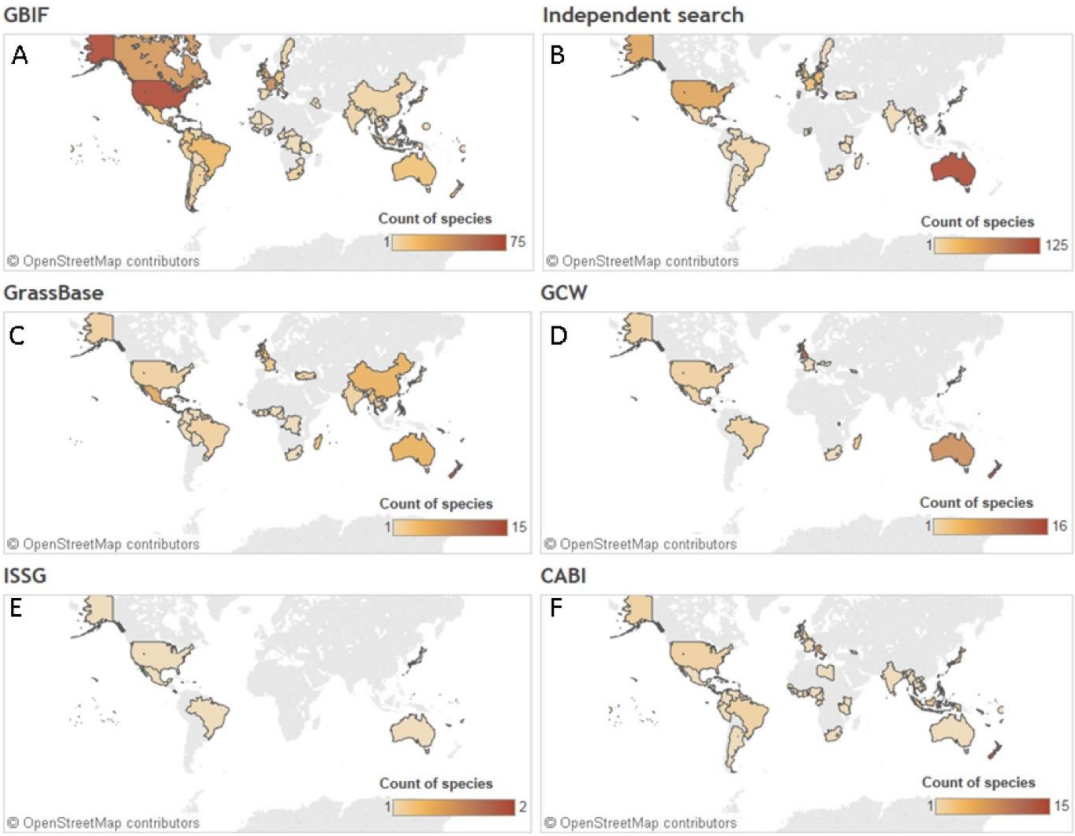
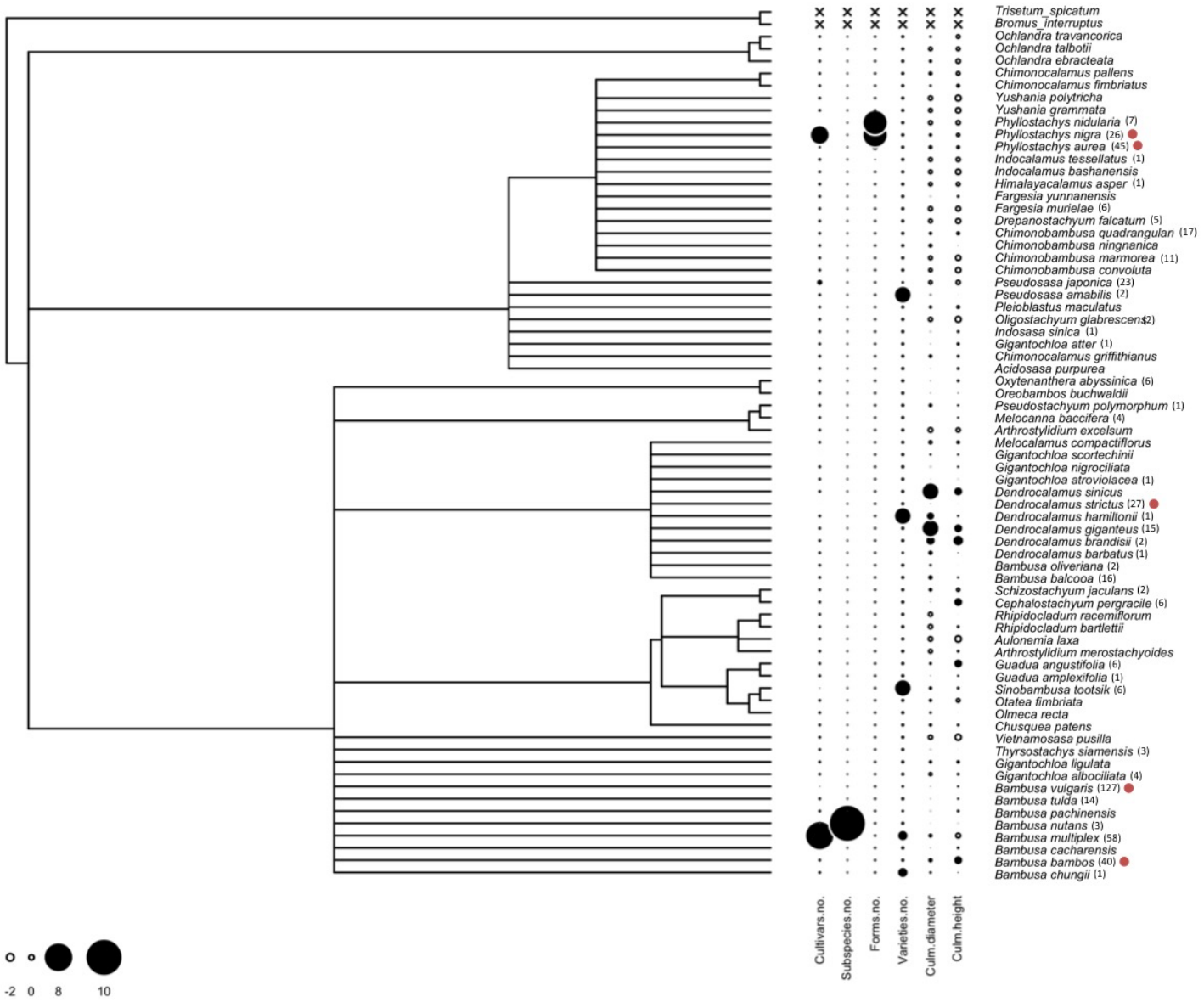


File S2.4 Species richness maps indicating the global geographic distribution of non-native bamboos by database sources: (A) Global Biodiversity Information Facility- GBIF, (B) an independent search for literature, (C) Kew's GrassBase, (D) Global Compendium of Weeds (GCW), (5) IUCN/ SSC Invasive Species Specialist Group (ISSG), and (F) Invasive Species Compendium- CABI.



File S2.5 Phylogenetic tree of 122 bamboo taxa built using collated genetic data for one chloroplast gene region, maturase K (*matK*). All sequences were retrieved from the online GenBank repository (ncbi.nlm.nih.gov). Six variables are shown I columns alongside tree branches showing cultivars no. (number of cultivars), subspecies no, (number of subspecies), forms no. (number of forms), varieties no. (number of genetic varieties), culm diameter (mac culm diameter) and culm height (max culm height) of corresponding species. Data in each column is scaled, where large black-filled circles indicate a higher quantity and white-filled circle indicate a smaller quantity of the particular variable associated with the given species relative to other taxa. Numbers after species names indicate the number of regions of introduction and red circles indicate invasive species.

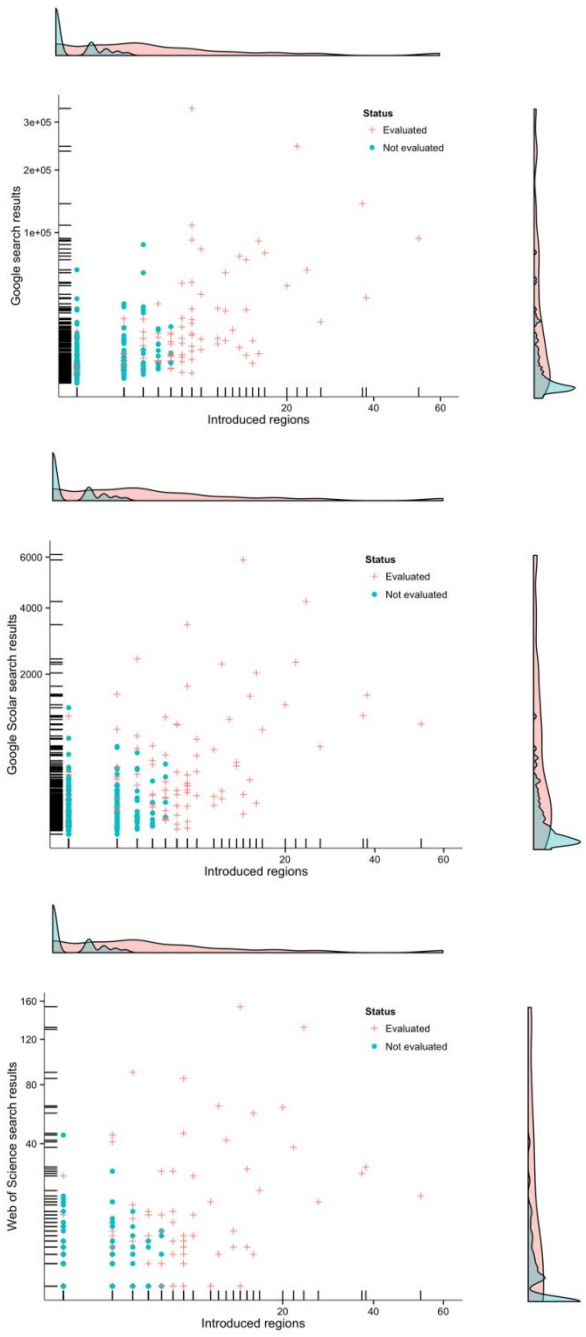


Figure S3.1 The relationship between the number of regions to which a species has been introduced and the number of search results returned on the online platforms of (a) Google (b) Google Scholar and (c) Web of Science. Occurrence points are divided into those that were actively searched for literature (or evaluated: red crosses) in the study and those that were not (not evaluated: blue circles).

Table S3.1 Number of environmental impact references reported in the native and alien range per species of bamboo.

Species	References	
	Alien	Native
Bambusa longispiculata	1	
Bambusa tulda	1	1
Bambusa tuldoides	2	
Bambusa vulgaris	7	
Cephalostachyum pergracile		1
Chusquea ramosissima		2
Dendrocalmus strictus	1	
Gigantochloa albociliata		1
Guadua sarcocarpa		1
Guadua tagoara		1
Guadua weberbaueri		1
Melocanna baccifera		1
Phyllostachys aurea	1	
Phyllostachys bambusoides		3
Phyllostachys edulis	16	15
Phyllostachys nigra	3	
Phyllostachys sp.	2	2
Pleioblastus chino		2
Sasa chartacea		1
Sasa kurilensis		1
Sasa palmata		1
Sasa sp.		1

Table S3.2 Number of environmental impact references per region and country.

Region	Country	References	
		Native	*Alien*
Africa	Nigeria		1
	Seychelles		1
Asia	China	16	
	India	1	
	Japan	8	15
	Taiwan		2
	Thailand	2	
North & Central America	Puerto Rico		2
	Trinidad & Tobago		2
	United States		3
Oceania	Hawaii, US		2
South America	Argentina	2	
	Brazil	2	2
	Peru	1	

File S4.1 List of tall-statured grasses (TSGs; 929 species). We define tall-statured grass species as those that normally attain self-sustaining heights of 2 m or more. Height data was retrieved from Kew's GrassBase (http://www.kew.org/data/grasses-db.html). Species names were cleaned, updated and corrected our species list (synonyms listed in brackets following the updated species name, where applicable); non-bamboo grasses were checked for synonyms using Kew's world checklist of selected plant families (http://apps.kew.org/wcsp/qsearch.do) and bamboo species were checked using the International Network for Bamboo and Rattan's (INBAR) global 2017 checklist.

Acidosasa breviclavata
Acidosasa chinensis
Acidosasa edulis
Acidosasa glauca (= Acidosasa chinouensis)
Acidosasa guangxiensis
Acidosasa lingchuanensis
Acidosasa nanunica
Acidosasa notata (= Pleioblastus intermedius)
Acidosasa purpurea
Actinocladum verticillatum
Ampelocalamus hirsutissimus
Ampelocalamus melicoideus
Ampelocalamus mianningensis
Ampelocalamus microphyllus
Ampelocalamus naibunensis
Ampelocalamus patellaris
Ampelocalamus saxatilis
Ampelocalamus yongshanensis
Andropogon bicornis
Andropogon chevalieri
Andropogon cordatus
Andropogon gabonensis
Andropogon gayanus
Andropogon incomptus
Andropogon macrophyllus
Andropogon monocladus
Andropogon tectorum
Andropogon vetus (= Andropogon perdignus)
Apoclada simplex
Arundinaria gigantea
Arundinella cochinchinensis
Arundinella decempedalis
Arundinella deppeana
Arundo donax
Arundoclaytonia dissimilis
Aulonemia amplissima
Aulonemia herzogiana
Aulonemia longiaristata
Aulonemia nitida
Aulonemia parviflora
Aulonemia queko
Aulonemia radiata (= Aulonemia fimbriatifolia)
Aulonemia robusta
Aulonemia ulei
Aulonemia viscosa
Austroderia fulvida (= Cortaderia fulvida)
Austrostipa elegantissima (= Stipa elegantissima)
Bambusa affinis
Bambusa albolineata
Bambusa amplexicaulis
Bambusa angustiaurita
Bambusa angustissima
Bambusa arnhemica
Bambusa aurinuda
Bambusa australis
Bambusa balcooa
Bambusa bambos
Bambusa basihirsuta
Bambusa beecheyana
Bambusa bicicatricata
Bambusa boniopsis
Bambusa brunneoaciculia
Bambusa burmanica
Bambusa cacharensis
Bambusa cerosissima
Bambusa chungii
Bambusa chunii
Bambusa clavata
Bambusa comillensis
Bambusa contracta
Bambusa copelandii
Bambusa corniculata
Bambusa cornigera
Bambusa crispiaurita
Bambusa diaoluoshanensis
Bambusa dissimulator
Bambusa distegia
Bambusa dolichoclada
Bambusa duriuscula
Bambusa eutuldoides
Bambusa farinacea
Bambusa fimbriligulata
Bambusa flexuosa
Bambusa funghomii
Bambusa gibba
Bambusa gibboides
Bambusa glabrovagina
Bambusa glaucophylla
Bambusa grandis
Bambusa guangxiensis
Bambusa heterostachya
Bambusa indigena
Bambusa insularis
Bambusa intermedia
Bambusa jacobsii
Bambusa jaintiana (= Bambusa alamii)
Bambusa khasiana
Bambusa kingiana
Bambusa lako
Bambusa lapidea
Bambusa latideltata
Bambusa laxa
Bambusa lenta
Bambusa longipalea
Bambusa longispiculata
Bambusa macrotis
Bambusa maculata
Bambusa malingensis
Bambusa microcephala
Bambusa mollis
Bambusa multiplex
Bambusa mutabilis
Bambusa nepalensis
Bambusa nutans
Bambusa odashimae
Bambusa oldhamii
Bambusa oliveriana
Bambusa pachinensis
Bambusa pallida
Bambusa papillata
Bambusa papillatoides
Bambusa pervariabilis
Bambusa pierreana
Bambusa piscatorum
Bambusa polymorpha
Bambusa procera
Bambusa prominens
Bambusa ramispinosa
Bambusa remotiflora
Bambusa riauensis
Bambusa rigida
Bambusa rongchengensis
Bambusa rugata
Bambusa rutila
Bambusa salarkhanii
Bambusa schizostachyoides
Bambusa semitecta
Bambusa sinospinosa
Bambusa stenoaurita
Bambusa subaequalis
Bambusa subtruncata
Bambusa surrecta
Bambusa teres
Bambusa textilis
Bambusa truncata
Bambusa tsangii
Bambusa tulda
Bambusa tuldoides
Bambusa utilis
Bambusa valida
Bambusa variostriata
Bambusa vinhphuensis
Bambusa viridis
Bambusa vulgaris
Bambusa wenchouensis

Bambusa xiashanensis
Bambusa xueana
Bashania qingchengshanensis (= Arundinaria qingchengshanensis)
Bergbambos tessellata (= Thamnocalamus tessellatus)
Bonia amplexicaulis
Bonia saxatilis
Bonia tonkinensis
Calamagrostis mesathera
Cathariostachys capitata
Cenchrus americanus (= Pennisetum glaucum)
Cenchrus elegans (= Pennisetum macrostachyum)
Cenchrus latifolius (= Pennisetum latifolium)
Cenchrus macrourus (= Pennisetum macrourum)
Cenchrus michoacanus (= Pennisetum crinitum)
Cenchrus nervosus (= Pennisetum nervosum)
Cenchrus peruvianus (= Pennisetum peruvianum)
Cenchrus pirottae (= Pennisetum pirottae)
Cenchrus preslii (= Pennisetum bambusiforme)
Cenchrus prolificus (= Pennisetum prolificum)
Cenchrus sieberianus (= Pennisetum sieberianum)
Cenchrus trisetus (= Pennisetum trisetum)
Cenchrus tristachyus (= Pennisetum tristachyum)
Cenchrus unisetus (= Pennisetum unisetum)
Cephalostachyum burmanicum
Cephalostachyum chinense (= Schizostachyum chinense)
Cephalostachyum flavescens
Cephalostachyum sanguineum (= Schizostachyum sanguineum)
Chasmopodium afzelii
Chasmopodium caudatum
Chimonobambusa angustifolia
Chimonobambusa armata
Chimonobambusa brevinoda
Chimonobambusa callosa
Chimonobambusa communis
Chimonobambusa convoluta
Chimonobambusa fansipanensis
Chimonobambusa grandifolia
Chimonobambusa hejiangensis
Chimonobambusa hirtinoda
Chimonobambusa hsuehiana
Chimonobambusa lactistriata
Chimonobambusa leishanensis
Chimonobambusa luzhiensis
Chimonobambusa macrophylla
Chimonobambusa marmorea
Chimonobambusa metuoensis
Chimonobambusa microfloscula
Chimonobambusa montigena
Chimonobambusa ningnanica
Chimonobambusa opienensis
Chimonobambusa pachystachys
Chimonobambusa paucispinosa
Chimonobambusa puberula
Chimonobambusa pubescens
Chimonobambusa purpurea
Chimonobambusa quadrangularis
Chimonobambusa rigidula
Chimonobambusa szechuanensis
Chimonobambusa tuberculata
Chimonobambusa tumidissinoda
Chimonobambusa utilis
Chimonocalamus baviensis (= Arundinaria baviensis)
Chimonocalamus burmaensis
Chimonocalamus delicatus
Chimonocalamus dumosus
Chimonocalamus fimbriatus
Chimonocalamus gallatlyi
Chimonocalamus griffithianus
Chimonocalamus longiligulatus
Chimonocalamus longiusculus
Chimonocalamus makuanensis
Chimonocalamus montanus
Chimonocalamus nagalandianus
Chimonocalamus pallens
Chionachne cyathopoda
Chionachne macrophylla
Chrysopogon elongatus
Chrysopogon festucoides
Chrysopogon nigritanus
Chrysopogon verticillatus
Chrysopogon zizanioides
Chusquea abietifolia
Chusquea albilanata
Chusquea anelytroides
Chusquea angusta (= Neurolepis angusta)
Chusquea antioquensis
Chusquea aristata (= Neurolepis aristata)
Chusquea asymmetrica (= Neurolepis asymmetrica)
Chusquea bilimekii
Chusquea caparaoensis
Chusquea circinata
Chusquea culeou
Chusquea cumingii
Chusquea erecta
Chusquea fernandeziana

Chusquea fimbriligulata (= Neurolepis fimbriligulata)
Chusquea juergensii
Chusquea lehmannii
Chusquea longiligulata
Chusquea longipendula
Chusquea lorentziana
Chusquea maclurei
Chusquea magnifolia (= Neurolepis pittieri)
Chusquea meyeriana
Chusquea mimosa
Chusquea mollis (= Neurolepis mollis)
Chusquea neurophylla
Chusquea nutans
Chusquea paludicola
Chusquea patens
Chusquea perotensis
Chusquea peruviana
Chusquea petiolata (= Neurolepis petiolata)
Chusquea polyclados
Chusquea spectabilis (= Neurolepis aperta)
Chusquea spencei
Chusquea subtessellata
Chusquea subtilis
Chusquea subulata
Chusquea sulcata
Chusquea talamancensis
Chusquea tarmensis
Chusquea tessellata
Chusquea tonduzii
Chusquea uliginosa
Chusquea vulcanalis
Coelorachis afraurita
Coelorachis balansae
Coelorachis glandulosa
Coelorachis khasiana
Coelorachis rottboellioides
Cortaderia atacamensis
Cortaderia bifida
Cortaderia jubata
Cortaderia richardii
Cortaderia selloana
Cortaderia speciosa
Cortaderia splendens
Cortaderia toetoe
Cymbopogon flexuosus
Cymbopogon giganteus
Cymbopogon martini
Cymbopogon winterianus
Cyrtochloa major
Danthoniopsis simulans
Davidsea attenuata
Dendrocalamus asper
Dendrocalamus bambusoides
Dendrocalamus barbatus
Dendrocalamus brandisii
Dendrocalamus buar
Dendrocalamus calostachyus
Dendrocalamus cinctus
Dendrocalamus elegans
Dendrocalamus exauritus (= Drepanostachyum exauritum)
Dendrocalamus farinosus
Dendrocalamus fugongensis
Dendrocalamus giganteus
Dendrocalamus hait
Dendrocalamus hamiltonii (= Dendrocalamus semiscandens)
Dendrocalamus hamiltonii (= Dendrocalamus semiscandens)
Dendrocalamus hirtellus
Dendrocalamus hookeri
Dendrocalamus jianshuiensis
Dendrocalamus liboensis
Dendrocalamus longispathus
Dendrocalamus membranaceus
Dendrocalamus messeri
Dendrocalamus minor
Dendrocalamus nudus
Dendrocalamus pachystachyus
Dendrocalamus peculiaris
Dendrocalamus pendulus
Dendrocalamus poilanei
Dendrocalamus pulverulentus
Dendrocalamus sahnii
Dendrocalamus sericeus
Dendrocalamus sikkimensis
Dendrocalamus sinicus
Dendrocalamus somdevae
Dendrocalamus strictus
Dendrocalamus tibeticus
Dendrocalamus tomentosus
Dendrocalamus tsiangii
Dendrocalamus yunnanicus
Didymogonyx longispiculatum (= Rhipidocladum longispiculatum)
Digitaria pellita
Diplachne gigantea (= Leptochloa gigantea)
Drepanostachyum ampullare
Drepanostachyum annulatum
Drepanostachyum falcatum
Drepanostachyum fractiflexum
Drepanostachyum intermedium
Drepanostachyum khasianum
Drepanostachyum semiorbiculatum
Echinochloa pyramidalis
Elymandra gossweileri
Elymandra subulata
Eremocaulon aureofimbriatum
Eremocaulon capitatum
Fargesia acuticontracta
Fargesia albocerea
Fargesia altior
Fargesia angustissima
Fargesia brevissima
Fargesia caduca
Fargesia canaliculata
Fargesia circinata
Fargesia communis
Fargesia concinna
Fargesia conferta
Fargesia contracta
Fargesia cuspidata
Fargesia declivis
Fargesia decurvata
Fargesia denudata
Fargesia dulcicula
Fargesia dura
Fargesia edulis
Fargesia elegans
Fargesia exposita
Fargesia extensa
Fargesia farcta
Fargesia ferax
Fargesia fungosa
Fargesia glabrifolia
Fargesia gongshanensis
Fargesia grossa
Fargesia hainanensis
Fargesia hsuehiana
Fargesia hygrophila
Fargesia jiulongensis
Fargesia lincangensis
Fargesia longiuscula
Fargesia lushuiensis
Fargesia macclureana

Fargesia mali
Fargesia murielae
Fargesia nitida (= Fargesia emaculata)
Fargesia nujiangensis
Fargesia obliqua
Fargesia orbiculata
Fargesia papyrifera
Fargesia perlonga
Fargesia pleniculmis
Fargesia plurisetosa
Fargesia porphyrea
Fargesia praecipua
Fargesia qinlingensis
Fargesia rufa
Fargesia sagittatinea
Fargesia scabrida
Fargesia semicoriacea
Fargesia similaris
Fargesia solida
Fargesia stenoclada
Fargesia strigosa
Fargesia subflexuosa
Fargesia sylvestris
Fargesia tenuilignea
Fargesia utilis
Fargesia wuliangshanensis
Fargesia yuanjiangensis
Fargesia yulongshanensis
Fargesia yunnanensis
Fargesia zayuensis
Ferrocalamus rimosivaginus
Ferrocalamus strictus
Gaoligongshania megalothyrsa
Gelidocalamus kunishii
Gelidocalamus latifolius
Gelidocalamus longiinternodus
Gelidocalamus solidus (= Gelidocalamus albopubescens)
Gelidocalamus solidus (= Gelidocalamus albopubescens)
Gelidocalamus stellatus
Gelidocalamus tessellatus (= Gelidocalamus subsolidus)
Gelidocalamus velutinus
Gigantochloa achmadii
Gigantochloa albociliata
Gigantochloa albopilosa
Gigantochloa albovestita
Gigantochloa apus
Gigantochloa atroviolacea
Gigantochloa atter
Gigantochloa aya
Gigantochloa baliana
Gigantochloa balui
Gigantochloa calcicola
Gigantochloa cochinchinensis
Gigantochloa compressa
Gigantochloa densa
Gigantochloa felix
Gigantochloa hasskarliana
Gigantochloa hirtinoda
Gigantochloa holttumiana
Gigantochloa kuring
Gigantochloa latifolia
Gigantochloa levis
Gigantochloa ligulata
Gigantochloa longiprophylla
Gigantochloa luteostriata
Gigantochloa macrostachya
Gigantochloa magentea
Gigantochloa manggong
Gigantochloa membranoidea
Gigantochloa multiculmis
Gigantochloa nigrociliata
Gigantochloa papyracea
Gigantochloa poilanei
Gigantochloa pruriens
Gigantochloa pubipetiolata
Gigantochloa ridleyi
Gigantochloa robusta
Gigantochloa rostrata
Gigantochloa scortechinii
Gigantochloa serik
Gigantochloa taluh
Gigantochloa thoi
Gigantochloa tomentosa
Gigantochloa velutina
Gigantochloa verticillata
Gigantochloa vietnamica
Gigantochloa vinhphuica
Glaziophyton mirabile
Greslania rivularis
Guadua amplexifolia
Guadua angustifolia
Guadua calderoniana
Guadua chacoensis
Guadua latifolia
Guadua longifolia
Guadua macclurei
Guadua macrostachya
Guadua paniculata
Guadua paraguayana
Guadua refracta
Guadua sarcocarpa
Guadua superba
Guadua tagoara
Guadua trinii
Guadua velutina
Guadua virgata
Guadua weberbaueri
Gynerium sagittatum
Himalayacalamus asper
Himalayacalamus brevinodus
Himalayacalamus collaris
Himalayacalamus cupreus
Himalayacalamus falconeri
Himalayacalamus fimbriatus
Himalayacalamus hookerianus
Himalayacalamus porcatus
Holttumochloa magica
Hymenachne pernambucensis (= Panicum pernambucense)
Hyparrhenia coriacea
Hyparrhenia cyanescens
Hyparrhenia cymbaria
Hyparrhenia dichroa
Hyparrhenia diplandra
Hyparrhenia gossweileri
Hyparrhenia madaropoda
Hyparrhenia rudis
Hyparrhenia schimperi
Hyparrhenia subplumosa
Hyparrhenia variabilis
Hyperthelia colobantha
Hyperthelia cornucopiae
Hyperthelia dissoluta
Hyperthelia edulis
Indocalamus bashanensis
Indocalamus guangdongensis
Indocalamus hirsutissimus
Indocalamus hirtivaginatus
Indocalamus petelotii
Indocalamus pseudosinicus
Indocalamus quadratus
Indocalamus tessellatus
Indosasa angustata
Indosasa bacquangensis
Indosasa crassiflora
Indosasa gigantea
Indosasa glabrata
Indosasa hispida

Indosasa ingens
Indosasa lipoensis
Indosasa longispicata
Indosasa lunata
Indosasa parvifolia
Indosasa patens
Indosasa singulispicula
Indosasa sinica
Indosasa sondongensis
Indosasa spongiosa
Indosasa triangulata
Ischaemum amethystinum
Kinabaluchloa nebulosa
Kinabaluchloa wrayi
Kuruna densifolia (= Arundinaria densifolia)
Kuruna walkeriana (= Arundinaria wightiana)
Leymus condensatus
Loudetia flammida
Loudetia phragmitoides
Loudetiopsis thoroldii
Melocanna arundina
Melocanna baccifera
Merostachys abadiana
Merostachys annulifera
Merostachys argentea
Merostachys brevispica
Merostachys burmanii
Merostachys calderoniana
Merostachys ciliata
Merostachys claussenii
Merostachys filgueirasii
Merostachys kunthii
Merostachys lanata
Merostachys latifolia
Merostachys leptophylla
Merostachys magellanica
Merostachys maguireorum
Merostachys medullosa
Merostachys multiramea
Merostachys neesii
Merostachys petiolata
Merostachys pilifera
Merostachys polyantha
Merostachys retrorsa
Merostachys riedeliana
Merostachys skvortzovii
Merostachys sparsiflora
Merostachys speciosa
Merostachys ternata
Miscanthus ecklonii
Miscanthus floridulus
Miscanthus fuscus
Miscanthus junceus
Miscanthus lutarioriparius
Miscanthus violaceus
Muhlenbergia gigantea
Muhlenbergia mutica
Muhlenbergia robusta
Myriocladus cardonae
Myriocladus churunensis
Myriocladus distantiflorus
Myriocladus exsertus
Myriocladus grandifolius
Myriocladus longiramosus
Myriocladus paludicola
Myriocladus virgatus
Nastus elatoides
Nastus elatus
Neohouzeaua helferi
Neohouzeaua kerriana
Neohouzeaua mekongensis
Neohouzeaua stricta
Neohouzeaua tavoyana
Neololeba amahussana (= Bambusa amahussana)
Neololeba hirsuta
Neyraudia arundinacea
Neyraudia curvipes
Neyraudia reynaudiana
Ochlandra ebracteata
Ochlandra keralensis
Ochlandra scriptoria
Ochlandra setigera
Ochlandra spirostylis
Ochlandra stridula
Ochlandra talbotii
Ochlandra travancorica (= Ochlandra sivagiriana)
Oldeania alpina (= Yushania alpina)
Oligostachyum gracilipes
Oligostachyum hupehense
Oligostachyum lanceolatum
Oligostachyum lubricum
Oligostachyum nuspiculum
Oligostachyum oedogonatum
Oligostachyum paniculatum
Oligostachyum scopulum
Oligostachyum shiuyingianum
Oligostachyum spongiosum
Oligostachyum sulcatum
Oligostachyum wuyishanicum
Olmeca clarkiae (= Aulonemia clarkiae)
Oryza grandiglumis
Oryza latifolia
Otatea acuminata (= Otatea aztecorum)
Otatea fimbriata
Otatea glauca
Oxytenanthera abyssinica
Panicum petersonii
Panicum tamaulipense
Paspalum cinerascens
Paspalum haumanii
Paspalum turriforme
Pentameris thuarii
Perrierbambus madagascariensis
Perrierbambus tsarasaotrensis
Phacelurus gabonensis
Phaenosperma globosum
Phragmites australis
Phragmites karka
Phragmites mauritianus
Phyllosasa tranquillans
Phyllostachys acuta
Phyllostachys angusta
Phyllostachys arcana
Phyllostachys atrovaginata
Phyllostachys aurea
Phyllostachys aureosulcata
Phyllostachys bissetii
Phyllostachys carnea
Phyllostachys circumpilis
Phyllostachys dulcis
Phyllostachys edulis
Phyllostachys elegans
Phyllostachys fimbriligula
Phyllostachys flexuosa
Phyllostachys glabrata
Phyllostachys glauca
Phyllostachys incarnata
Phyllostachys iridescens
Phyllostachys kwangsiensis
Phyllostachys lofushanensis
Phyllostachys makinoi
Phyllostachys mannii
Phyllostachys meyeri
Phyllostachys nidularia
Phyllostachys nigella
Phyllostachys nigra (= Phyllostachys guizhouensis)
Phyllostachys nuda

Phyllostachys parvifolia
Phyllostachys platyglossa
Phyllostachys prominens
Phyllostachys propinqua
Phyllostachys reticulata
Phyllostachys rivalis
Phyllostachys robustiramea
Phyllostachys rubicunda
Phyllostachys rutila
Phyllostachys shuchengensis
Phyllostachys stimulosa
Phyllostachys sulphurea
Phyllostachys tianmuensis
Phyllostachys varioauriculata
Phyllostachys veitchiana
Phyllostachys verrucosa
Phyllostachys violascens
Phyllostachys virella
Phyllostachys viridiglaucescens
Phyllostachys vivax
Phyllostachys yunhoensis
Pleioblastus altiligulatus
Pleioblastus amarus
Pleioblastus argenteostriatus (= Arundinaria chino)
Pleioblastus gramineus (= Arundinaria graminea)
Pleioblastus hsienchuensis
Pleioblastus incarnatus
Pleioblastus kodzumae (= Arundinaria kodzumae)
Pleioblastus linearis (= Arundinaria linearis)
Pleioblastus maculatus
Pleioblastus matsunoi (= Arundinaria matsunoi)
Pleioblastus rugatus
Pleioblastus sanmingensis
Pleioblastus simonii (= Arundinaria simonii)
Pleioblastus solidus
Pleioblastus truncatus
Pleioblastus wuyishanensis
Pleioblastus yixingensis
Pseudosasa aeria
Pseudosasa amabilis
Pseudosasa japonica
Pseudosasa longiligula
Pseudosasa maculifera
Pseudosasa nabeshimana
Pseudosasa orthotropa
Pseudosasa subsolida
Pseudosasa viridula
Pseudosasa wuyiensis
Pseudoxytenanthera ritcheyi
Pseudoxytenanthera stocksii
Racemobambos novohibernica
Rhipidocladum bartlettii
Rhipidocladum clarkiae
Rhipidocladum harmonicum
Rhipidocladum pacuarense
Rhipidocladum panamense
Rhynchoryza subulata
Saccharum × sinense
Saccharum alopecuroides
Saccharum arundinaceum
Saccharum asperum
Saccharum beccarii
Saccharum bengalense
Saccharum giganteum
Saccharum longisetosum
Saccharum maximum
Saccharum narenga
Saccharum officinarum
Saccharum procerum
Saccharum ravennae
Saccharum robustum
Saccharum rufipilum
Saccharum spontaneum
Saccharum stewartii
Saccharum wardii
Sarocalamus spanostachyus (= Arundinaria spanostachya)
Sasa palmata (= Sasa cernua)
Sasa suzukii
Sasa tomentosa
Sasa tsuboiana
Sasaella bitchuensis (= Sasa bitchuensis)
Sasaella masamuneana (= Sasa masamuneana)
Schizostachyum aequiramosum
Schizostachyum andamanicum
Schizostachyum atrocingulare
Schizostachyum auriculatum
Schizostachyum bamban
Schizostachyum beddomei
Schizostachyum blumei
Schizostachyum brachycladum
Schizostachyum castaneum
Schizostachyum caudatum
Schizostachyum copelandii
Schizostachyum coradatum (= Neohouzeaua coradata)
Schizostachyum cuspidatum
Schizostachyum diffusum
Schizostachyum distans
Schizostachyum dumetorum
Schizostachyum flexuosum
Schizostachyum funghomii
Schizostachyum glaucifolium
Schizostachyum glaucocladum
Schizostachyum gracile
Schizostachyum grande
Schizostachyum griffithii
Schizostachyum hainanense
Schizostachyum hantu
Schizostachyum insulare
Schizostachyum iraten
Schizostachyum jaculans
Schizostachyum kalpongianum
Schizostachyum khoonmengii
Schizostachyum latifolium
Schizostachyum lengguanii
Schizostachyum lima
Schizostachyum lumampao
Schizostachyum lutescens
Schizostachyum mampouw
Schizostachyum pergracile (= Cephalostachyum pergracile)
Schizostachyum perrieri
Schizostachyum pilosum
Schizostachyum pseudolima
Schizostachyum rogersii
Schizostachyum silicatum
Schizostachyum tessellatum

Schizostachyum zollingeri
Semiarundinaria fastuosa
Semiarundinaria fortis
Semiarundinaria kagamiana
Semiarundinaria shapoensis
Semiarundinaria sinica
Semiarundinaria yashadake
Setaria grandis
Setaria megaphylla
Sinobambusa baccanensis
Sinobambusa farinosa
Sinobambusa henryi
Sinobambusa incana
Sinobambusa intermedia
Sinobambusa nephroaurita
Sinobambusa solearis
Sinobambusa tootsik
Sinobambusa yixingensis
Sorghum × almum)
Sorghum amplum
Sorghum arundinaceum
Sorghum bicolor
Sorghum exstans
Sorghum grande
Sorghum intrans
Sorghum macrospermum
Sorghum plumosum
Sorghum propinquum
Sorghum stipoideum
Spodiopogon lacei
Sporobolus cynosuroides)
Sporobolus elatior
Sporobolus maximus
Stipa gigantea
Suddia sagittifolia
Thamnocalamus spathiflorus
Themeda caudata
Themeda cymbaria
Themeda gigantea
Themeda intermedia
Themeda novoguineensis
Themeda villosa
Thyrsostachys oliveri
Thyrsostachys siamensis
Thysanolaena latifolia
Triodia lanosa (= Symplectrodia lanosa)
Triodia longiloba
Triodia pascoeana
Triodia plectrachnoides
Tripsacum australe
Tripsacum cundinamarce
Tripsacum dactyloides
Tripsacum intermedium
Tripsacum jalapense
Tripsacum latifolium
Tripsacum laxum
Tripsacum pilosum
Trisetum virletii
Urelytrum giganteum
Valiha diffusa
Vietnamocalamus catbaensis
Yushania addingtonii
Yushania ailuropodina
Yushania anceps
Yushania bojieiana
Yushania brevipaniculata
Yushania burmanica
Yushania cartilaginea
Yushania cava
Yushania collina
Yushania complanata
Yushania crassicollis
Yushania crispata
Yushania dafengdingensis
Yushania elegans
Yushania elevata
Yushania exilis
Yushania falcatiaurita
Yushania farcticaulis
Yushania farinosa
Yushania flexa
Yushania glandulosa
Yushania glauca
Yushania grammata)
Yushania hirsuta
Yushania humbertii
Yushania lacera
Yushania laetevirens
Yushania levigata
Yushania lineolata
Yushania longiuscula
Yushania maculata
Yushania madagascariensis
Yushania maling
Yushania menghaiensis
Yushania mitis
Yushania multiramea
Yushania niitakayamensis
Yushania oblonga
Yushania pauciramificans
Yushania perrieri
Yushania rolloana
Yushania shangrilaensis
Yushania straminea
Yushania tessellata
Yushania velutina
Yushania vigens
Yushania wardii
Yushania wuyishanensis
Yushania xizangensis
Yushania yadongensis
Zea luxurians
Zea mays
Zea mexicana
Zea nicaraguensis
Zeugites hackelii
Zizania palustris
Zizaniopsis bonariensis
Zizaniopsis killipii
Zizaniopsis microstachya
Zizaniopsis miliacea

File S4.2. Additional information regarding Risk Assessment schemes (RAs) used to evaluate tall-statured grasses (TSGs)

Risk Assessment schemes (RAs) are often a modified version of the Australian Weed Risk Assessment model (A-WRA) developed by Pheloung et al. (1999). A number of RAs were used by several authors to evaluate the impact potential of TSG on all continents, i.e. AWRAM (Aquatic Weed Risk Assessment Model by Champion et al., 2010); C-WRA (Canada Weed Risk Assessment, modified version of the original A-WRA to evaluate alien plants in Canada by Mc Clay et al., 2010); H-WRA (Hawaiian Weed Risk Assessment, a modified version of the original A-WRA to evaluated the ecosystems of Hawaii and the Pacific Islands by Daehler et al., 2004); I-WRA (Italian Weed Risk Assessment, modified of the original A-WRA to evaluate alien plants in Tuscany, Italy by Lazzaro et al., 2016); J-WRA (Japanese Weed Risk Assessment, modified version of the original A-WRA to evaluate alien plants in Japan by Nishida et al., 2009); US-WRA (U.S Weed Risk Assessment, modified version of the original A-WRA for separate evaluation at the state and national scales in US by Gordon et al., 2011); USAqWRA (US Aquatic Weed Risk Assessment, modified version of the original A-WRA to evaluate alien aquatic plants in U.S by Gordon et al., 2012, then applied in South America by Lozano and Brundu (2018); WRA-ChAr (Weed Risk Assessment-Chile-Argentina, modified version of the original A-WRA to evaluate alien plants in Chile and Argentina by Fuentes et al., 2010); M-WRA (Mediaterranean Weed Risk Assessment, modified version of the original A-WRA to evaluate alien plants in Spain by Gassó et al., 2010); WG-WRA (Risk Assessment for Central Europe developed by Weber and Gut, 2004), also we considered the information from EPPO PRA (EPPO Pest Risk Analysis); PRE (Plant Risk Evaluation to evaluated the invasive potential to ornamental plants developed by Conser et al., 2015); PPQ WRA (Weed Risk Assessment Plant Protection and Quarantine, US Department of Agriculture, to evaluate the risk potential of plants, including those newly detected in the U.S) and ODA PRA (Oregon Department of Agriculture Plant Pest Risk Assessment. This Risk Assessment was modified by ODA from the USDA-APHIS Risk Assessment for the introduction of new plant species. The potential risk scores obtained from the RA schemes represent an outcome that classify different categories of invasion in the endangered area, e.g. HR (High Risk), EF (Evaluate Further), or LR (Low Risk). Accept, Reject or Evaluate. Invasive, Minor Concern (MC) or Lower Priority (LP). The higher the value (ranking for each RA), the greater the species invasiveness. In some cases a secondary screening was used i.e. if the species was classified as Evaluate Further by the main model, it undergoes a secondary screening process that focuses on a few factors that will be predictive of risk potential. Following secondary evaluation, species may be classified as HR (High Risk) or LR (Low Risk), Accepted or Reject.

File S4.3 The frequency of tall-statured grasses (TSGs) and non-TSGs in terms of their naturalisation success. Data are the number of species within categories that are reported as naturalised in at least one region of the world (n=843) in the GloNAF database (see van Kleunen et al. 2015 for details). Mean number ± S.E. of regions from which the species is recorded as naturalised is shown for species that appear in the GloNAF database. Note that the group of bamboos refers to species within the Bambuseae tribe, and non-bamboo grasses include all other grass tribes.

	Stature	Number of species			Percentage naturalised	Number of regions where naturalised
		Naturalised	Not naturalised	Total		
All grasses	TSG	106	823	929	11.4%	16.0±3.4
	non-TSG	1120	8769	9889	11.3%	20.7±1.2
Bamboos	TSG	57	692	749	7.6%	7.2±2.0
	non-TSG	8	394	402	2.0%	2.2±0.6
Non-bamboo grasses	TSG	49	131	180	27.2%	26.3±6.7
	non-TSG	1112	8375	9487	11.7%	20.8±1.2

Table S5.1. Facebook groups where the questionnaire was posted on, and the general outreach of each subsequent group reported by either members of the group or likes associated with the group. The outreach numbers are as recorded on the day the post was made between the 5th and 10th of May 2017.

Group name	Outreach		Link
ADS LIMPOPO	9299	members	https://www.facebook.com/groups/JOBSHERENOW/
AGFO Expo - Agriculture & Forestry	3612	likes	https://www.facebook.com/AGFOExpo/
Alien Plant Identification Services	275	likes	https://www.facebook.com/Alien-Plant-Identification-Services-369800736547050/
Ariston Elemental Organic Garden	573	likes	https://www.facebook.com/aristonelementalorganicgarden/
Bromeliads in South Africa	1626	members	https://www.facebook.com/groups/bromeliadsocietysa/
BUY AND SELL SOUTH AFRICA	16530	members	https://www.facebook.com/groups/831935736829559/
Cape Environmental Assessment Practitioners	91	likes	https://www.facebook.com/cape.eaprac/
Cape Town Invasive Species	2328	likes	https://www.facebook.com/ctinvasives/
Carnivorous Plant Growers South Africa	520	members	https://www.facebook.com/groups/7456615255507236/
Cycadfriends Community	3124	members	https://www.facebook.com/groups/CycadForumPetition/?ref=br_rs
Dam & River Angling in South Africa	14152	members	https://www.facebook.com/groups/Heenenr/?ref=br_rs
Department of Botany, Rhodes University	347	likes	https://www.facebook.com/BotanyRhodesUniversity/
Farmers Network South Africa (FNSA)	15149	members	https://www.facebook.com/groups/FarmersNetworkSouthAfrica/
Flora of Southern Africa	3515	members	https://www.facebook.com/groups/Floraofsouthernafrica/
Garden Technics SA	180	likes	https://www.facebook.com/gardentechnicssa/
Gauteng Conservancy and Stewardship Association	102	members	https://www.facebook.com/groups/630179793790090/about/
Hout Bay Organised	923	likes	https://www.facebook.com/groups/houtbay/
Howick (KZN South Africa)	1581	members	https://www.facebook.com/groups/663062110384807/
Indigenous Flowers of South Africa	2741	members	https://www.facebook.com/groups/IBSAgroup/about/
Invasive/Exotic Plant Species in South Africa	496	members	https://www.facebook.com/groups/2196045783373033/
Invasive Species South Africa (ISSA)	6651	likes	https://www.facebook.com/invasivespeciessouthafrica/

Group name	Outreach		Link
Joburg Online	6426	members	https://www.facebook.com/groups/joburgonline/
Klein Karoo Sustainable Drylands Permaculture Project	1511	members	https://www.facebook.com/groups/228236642394/
KZN Midlands seed savers	61	members	https://www.facebook.com/groups/222812881156285/?ref=br_rs
LETS TALK PLANTS, TREES AND SHRUBS	864	members	https://www.facebook.com/groups/treesandplants/
Limpopo Classifieds	12956	members	https://www.facebook.com/groups/325338070893306/
Livingseeds Veggie Gardeners	3824	members	https://www.facebook.com/groups/1149111552052 06/
MAMAHOOD FREE STATE	3282	members	https://www.facebook.com/groups/MamahoodFreeState/
Mbombela Invasives	190	likes	https://www.facebook.com/Mbombelainvasives/
MDMB Landscapes	269	likes	https://www.facebook.com/mdmblandscapes/
NACSSA National Association of Conservancies/ Stewardship South Africa	NA		https://www.facebook.com/NACSSA-National-Association-of-ConservanciesStewardship-South-Africa-134435801056/
Orchid growers South Africa	4864	members	https://www.facebook.com/groups/1326551202700 19/
Organic farmers of South Africa	5152	members	https://www.facebook.com/groups/OrganicFarmersZA/
Passionate about gardening South Africa	317	members	Passionate about gardening South Africa
Permaculture Network South Africa	812	members	https://www.facebook.com/groups/308946355788009/
Permaculture Research Centre Cape Town	3964	likes	https://www.facebook.com/PRCCapetown/
PETS and FARMERSGALORE [South Africa]	7016	members	https://www.facebook.com/groups/petsandfarmersgalore/
Plant People South Africa	4046	members	https://www.facebook.com/groups/plantpeoplesa/
Poultry Farming South Africa/ Africa	11911	members	https://www.facebook.com/groups/1670599293177361/about/
S.A. Butterflies, Bugs, Bees and other small things	21077	members	https://www.facebook.com/groups/Butterfliesandbugs/
Seed and Plant Exchange/ For Sale South Africa	3327	members	https://www.facebook.com/groups/836314193121949/
SOLVE- Save Our Limpopo Valley Environment	3321	members	https://www.facebook.com/groups/274439892602335/about/
SANA- South African Nursery Association	2935	followers	https://www.facebook.com/sanurseryassociation/?ref=br_rs
Sylvia Pass Garden Centre	145	likes	https://www.facebook.com/Sylvia-Pass-Garden-Centre-667658326717416/

Group name	Outreach		Link
The Botanical Society of South Africa	4473	members	https://www.facebook.com/BotSocSA/
The Sappi Nature Journal	1069	likes	https://www.facebook.com/The-Sappi-Nature-Journal-139925246217214/
Trade Board: Exotic, Rare and unusual plants	958	members	https://www.facebook.com/groups/795879563824370/
Urban Farmers	2392	likes	NA
URBAN FARMING- South Africa	471	members	https://www.facebook.com/groups/1042453599175549/
Vegetable, Fruit & Herb Gardening South Africa	123	members	https://www.facebook.com/groups/1156813641054679/
Veld/ vegetation of South Africa	443	members	https://www.facebook.com/groups/443110699189777/?ref=br_rs

Table S5.2. Literature referencing bamboo in South Africa, including the language of the literature (Afr=Afrikaans, Eng= English, Dut=Dutch), and the province (WC= Western Cape, KZN=KwaZulu-Natal, MPU= Mpumalanga, LIM=Limpopo) in which the bamboo is being used or cultivated. Ordered by earliest mention to the newest.

Reference	**Relevance**	**Species**	**Lang**	**Notes**	**Date used/ date planted (dp)**	**Province**
Leibbrandt 1990	Introduction history	General	Afr/ Eng	Introduction from India for building	1652-1662	WC
Spilhaus 1966	Introduction history	General	Eng	Import of bamboos by the VOC, and planting by Van Rieebeck	1653 (dp)	WC
Kolb 1726	Usage	General	Dut	Atjar	1727	WC
Thunberg 1795	Usage	General	Eng	Tools and utensils	1779	WC
Claassens and Pretorius 2004	Usage	General	Afr	Atchar pickled young bamboo shoots for food	c. 1800s	WC
Ferreira 1990	Usage	General	Afr	Garden ornamental	< 1816 (dp)	WC
Vahed 2009	Usage	General	Eng	Religious ornaments	1860-1910	-
McCracken 1886	Usage	General	Eng	Horticultural planting along roads	1870s	KZN
Ergates 1902	Usage	General	Eng	Fruit boxes, ladders, tools, wind break, poles	c. 1880 (dp)	KZN
Ergates 1906b	Usage	General (20 m high tropical type)	Eng	Walls, doors, ladders, water troughs, handles tools	c. 1880 (dp)	KZN
Kearney 1999	Usage	General	Eng	Religion flag poles	20th Century	KZN
Botes 2003	Usage	General	Afr	Furniture	Late 1900s-early 20th century	FS
Simpson 1904	Usage	General	Eng	Nets/ mosquito nets	1904	-
Legat 1905	Introduction history	12 species	Eng	Import of seeds and live plants from India	c. 1905 (dp)	-
Taylor 1910	Introduction history	*Dendrocalamus strictus*	Eng	Experimental plantation in nursery	1905 (dp)	MPU
Ergates 1906a	Usage	General	Eng	Cattle dipping tanks	1906	-

Reference	Relevance	Species	Lang	Notes	Date used/ date planted (dp)	Province
Braine 1907	Usage	General	Eng	Drainage in orchards	1907	-
Exchange Reviews 1908	Usage	General	Eng	Paper pulp	1908	-
Davies 1908	Cultivation	General	Eng	Experimental plantations	1908	KZN
Sawer 1909	Cultivation	General	Eng	Experimental plantations	1909	MPU
Davis 1910	Cultivation	*Dendrocalamus strictus*	Eng	Experimental plantation in nursery	1909 (dp)	MPU
Reid 1910	Cultivation	13 species listed	Eng	Experimental plantations	1910	KZN
Fletcher 1925	Usage	General	Eng	Crates for harvesting tobacco	1925	-
Terry 1927	Usage	General	Eng	Garden trellis	1927	KZN
Esselen 1930	Usage	General	Eng	Garden trellis	1930	-
Cleghorne 1931	Cultivation	General	Eng	Soil reclamation	1931	-
Clementz 1931	Cultivation	General	Eng	Building, vegetation for river ways, feed stock	1931	NC
Olivier 1938	Usage	General	Eng	Ostrich feather dusters	1938	-
du Plessis 1939	Usage	General	Eng	Vivoculture tools	1939	WC
Liengme 1983	Usage	General	Eng	Venda flutes	c. 1980s	LIM
van der Waal 1982	Usage	General	Afr	Hut building	1982	
Oosthuysen 2016	Cultivation	General	Afr	Sticks	1900s	WC
Milton 2004	Species list	-	Eng	Status of invasive and naturalised grasses	2004	-
Foxcroft et al. 2008	Species list	-	Eng	Status of invasive and naturalised grasses	2008	MPU
Visser et al. 2017	Species list	-	Eng	Status of invasive and naturalised grasses	2017	-
Glen 2002	Species list	16 species	Eng	-	-	-
Fowler 2008	Usage	General	Eng	Pottery tools	Current	KZN

Reference	Relevance	Species	Lang	Notes	Date used/ date planted (dp)	Province
University of Venda	Introduction history	*Oxytenanthera abyssinica*	Eng	-	-	-
Magwede 2018	Usage	*B. balcooa; Bambusa vulgaris*	Eng	Construction by the Venda	Current	LIM
Tangye 1896	Usage	Swiepstock bamboes	Afr	Whips	1900s	-

Table S5.3 Questionnaire targeting landowners in South Africa with bamboo on their property.

Name
Contact number
Contact email
Where did you hear about this research?
Age
What is your occupation?
In which province is the property located that has bamboo present on it?
How many types/ species of bamboo do you think are on the property?
What is the address or locality of the property with bamboo/s population? (GPS coordinates if possible)
What is the nearest town or city to your property?
What kind of property is the bamboo located on? (e.g. commercial farm, urban garden, smallholding etc.)
What is the primary use for the property?
What is your connection with the property?
Did you initially plant the bamboo? If not, do you know who did?
Do you know when the bamboo was first planted on the property? if you know the specific year, please write it in other.
Where was the bamboo planted?
Do you know what the original purpose for the bamboo was? (please click all relevant uses, if there are other specific uses, such as for candlesticks, write in 'other')
Is the bamboo a useful plant on the farm today?
How is the bamboo used today? (please click all relevant uses, and add specific uses in 'other')
How much space does the bamboo occupy currently? If you know the exact measurement, please write in 'other'
How many clumps or populations of bamboo are there?
How often do you use the bamboo on the property?
Do you have any interesting stories about the bamboo and/ or its history on the property or in South Africa, in general, that you would like to share?
Does the bamboo cause any problems?
If the bamboo is spreading, has it spread a distance of 2 meters or more per year from the original plant?
If problematic, please select and explain some of the ways it is a nuisance?
Would you consider the bamboo a weed (an undesirable plant)?
Have you tried to remove the population? if yes, what was the outcome?
How tall is the bamboo stand? If you can be specific, please answer under 'other'
How thick are the bamboo culms (or stalks)? Please give a specific answer if possible.
Have you ever observed the population flowering or producing seeds?
What colour are the culms or stalks of the bamboo?
What is the growth form of the bamboo?
Can you identify which species of bamboo are on the property from the pictures below?
If there is any other information you would like to share?
Would you like to be informed of any outputs (articles etc.) that may come of this research?

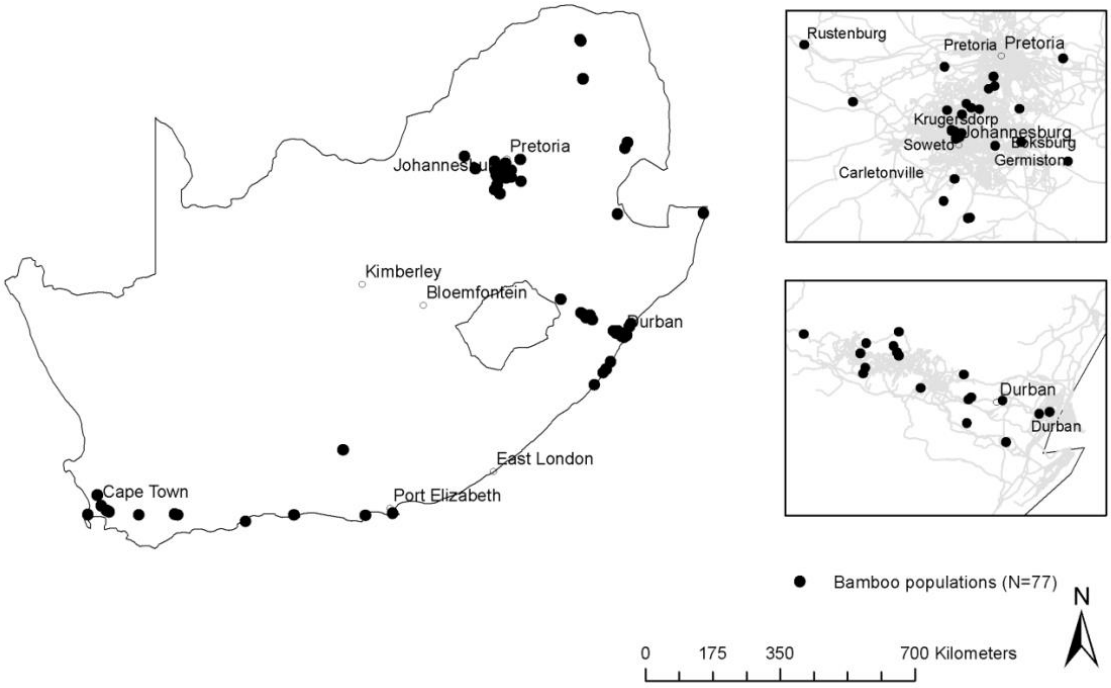


Fig S5.1. Localities of questionnaire respondents with bamboo on their property (n=77) were received for all South African provinces except the Northern Cape (four sites were excluded as locality information was not provided). Many responses were received from urban areas, especially Durban and Johannesburg.

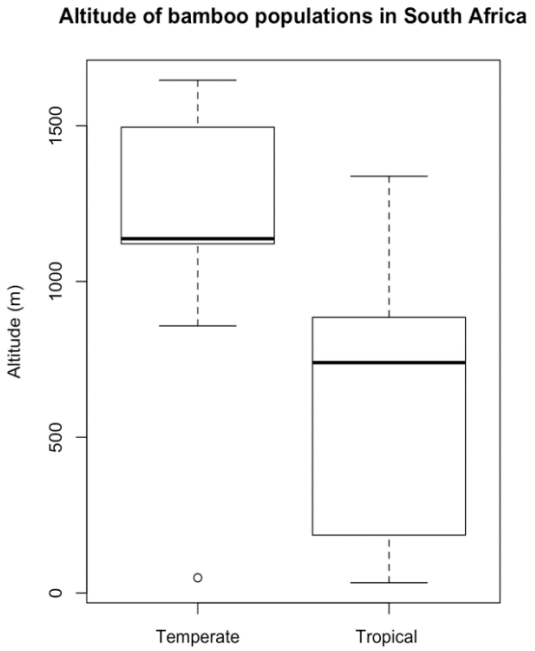


Figure S6.1. Altitude of alien bamboo populations observed during the study by lineage type (temperate or tropical) between the years 2014 to 2017.

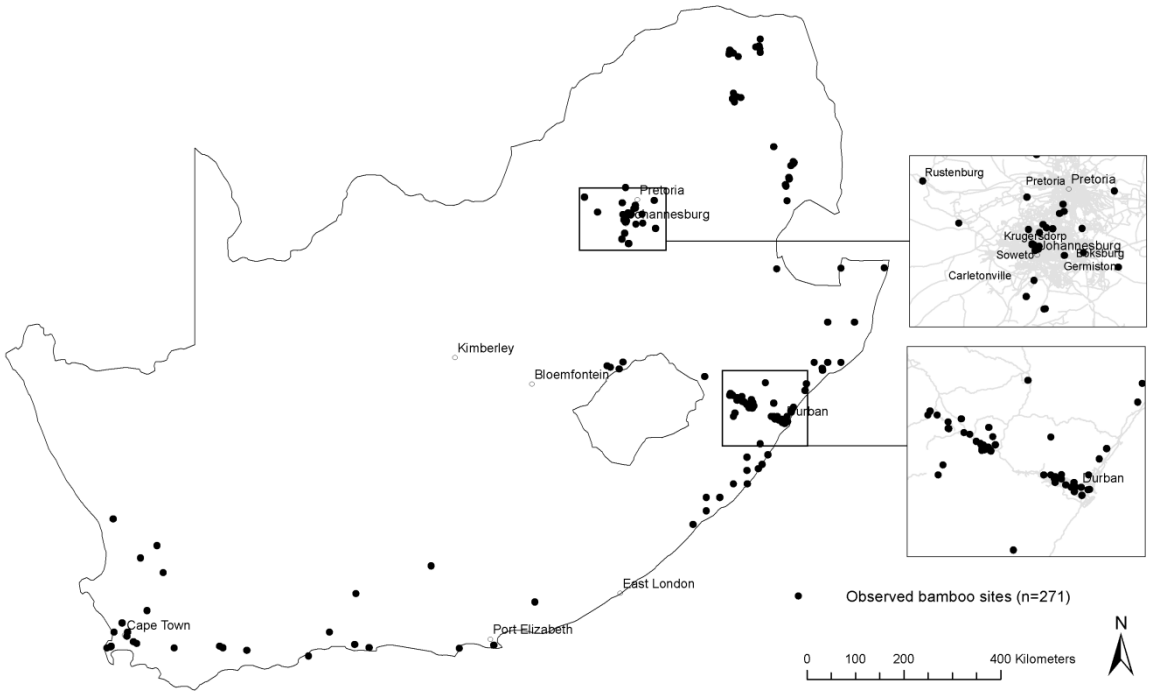


Figure S6.2. Observed populations of alien bamboo species across South Africa from 1896-2017. Data comes from a combination of sources including herbarium records (n=89), personal observations (n=106), and responses from an online questionnaire in 2017 (n=76).

Table S6.2 The test results of two bamboo samples collected during sampling that were sequenced using the D4 chloroplast region and BLAST on GenBank (28th July 2018; blast.ncbi.nlm.nih.gov/Blast.cgi) to compare with other species. The sequences of this region were found to match 100% with other closely related species, as well as species in entirely different genera and lineages, for both test samples.

Species	Sequence	Collection site	BLAST results with 100% match
Bambusa balcooa	TCCCTTCATTCTTCCTCTATGTTGTTTACG AAATCTGGTTCTTTTGGGGTTATAGTCGA TGGTTCTTTCTTAGTTCCATCTCTACTGCA AAACTGGACATGAGAGTTTCTTCTCATCC AGCTCCTCGCGAATGAAATGAGAAAGCG TGCAAATTTCTCTAATTCCATAATATTTT GGAATATTATGGATAGATGCACATTAAT AGATAATAGAAAAAGTTAGGGTTTTTTTA ATATTGAATATTGAATTTGTTAAAATAGA AAAATATATAGTCAAGAAAGAAGATCTA GAATATATCTAGATGTGTGTGTCTATTTA TCTATATTCTATATTTATAGATAATGTAA TCTTTCTTAAAAAAAAATCTCCTTATTTC GACTCTTATTGAATCGCGGGAAAGTATTC TAATTCAATAAAGATTTCGCGGGCGAAT ATTTACTCTTTCCTGTCTTATTTGTTAATT TATAACCTTACCAAATAAGGCAATTTTTT TGGTT	Stanger farm, along Nonoti river, KZN	*Chimonobambusa tumidissinoda; Phyllostachys aurea; Fargesia nitida; Yushania levigata; Fargesia yunnanensis; Fargesia spathacea; Fargesia nitida; Sarocalamus faberi; Phyllostachys sulphurea; Phyllostachys propinqua; Phyllostachys edulis; Indocalamus longiauritus; Phyllostachys nigra var. henonis*
Bambusa multiplex	TCTTCCTCTATGTTGTTTACGAAATCTGG TTCTTTTGGGGTTATAGTCGATGGTTCTTT CTTAGTTCCATCTCTACTGCAAAACTGGA CATGAGAGTTTCTTCTCATCCAGCTCCTC GCGAATGAAATGAGAAAGCGTGCAAATT TCTCTAATTCCATAATATTCCAAAATATT ATGGATAGATGCACATTAATAGATAATA GAAAAAGTTAGGGTTTTTTTAATATTGAA TTTGTTAAAATAGATAAATATATAGTCAA GAAAGAAGATCTAGAATATATCTAGATG TGTGTGTCTATTTATCTATATTCTATATTT ATGGATAATGTAATCTTTCTTAACAAAAA ATCTCCTTATTTTTACTCTTATTGAATCGC GGTAAAGTATTCTAATTCAATAAAGATTT CGCGGGCGAATATTTACTCTTTCCTGTCT TATTTGTTAATTTATATTATAACCTTACC AAATAAGGCAATTTTTTTGGTT	Fern Gully, Knysna, WC	*Phyllostachys edulis; Bambusa multiplex; Bambusa oldhamm; Bambusa ventricosa; Bambusa odashimae; Bambusa cornigera; Bambusa beecheyana; Bambusa basihirsuta*